

18 **Abstract**

19 Dinitrogen (N_2) and nitrous oxide (N_2O) produced via denitrification may represent major nitrogen
20 (N) loss in terrestrial ecosystems. A global assessment of soil denitrification rate, $N_2O/(N_2O+N_2)$
21 ratio, and their driving factors and mitigation strategies is lacking. We conducted a global synthesis
22 using 225 studies (3367 observations) to fill this knowledge gap. We found that daily N loss
23 through soil denitrification varied with ecosystems and averaged $0.25 \text{ kg N ha}^{-1}$. The average
24 emission factor of denitrification (EF_D) was 4.8%. The average $N_2O/(N_2O+N_2)$ ratio from soil
25 denitrification was 0.33. Soil denitrification rate was positively related to soil water-filled pore
26 space (WFPS) ($p<0.01$), nitrate (NO_3^-) content ($p<0.05$) and soil temperature ($p<0.01$), and
27 decreased with higher soil oxygen content ($p<0.01$). N_2 emissions increased with latitude ($p<0.05$),
28 WFPS ($p<0.01$) and soil mineral N ($p<0.05$) but decreased with soil oxygen content ($p<0.05$). The
29 $N_2O/(N_2O+N_2)$ ratio increased with soil oxygen content ($p<0.01$) but decreased with organic
30 carbon (C) ($p<0.05$), C/N ratio ($p<0.01$), soil pH ($p<0.05$) and WFPS ($p<0.01$). We also found that
31 optimizing N application rates, using ammonium-based fertilizers compared to nitrate-based
32 fertilizers, biochar amendment, and application of nitrification inhibitors could effectively reduce
33 soil denitrification rate and associated N_2 emissions. These findings highlight that N loss via soil
34 denitrification and N_2 emissions cannot be neglected, and that mitigation strategies should be
35 adopted to reduce N loss and improve N use efficiency. Our study presents a comprehensive data
36 synthesis for large-scale estimations of denitrification and the refinement of relevant parameters
37 used in the submodels of denitrification in process-based models.

38 **1 Introduction**

39 Denitrification is a microbial process by which nitrate (NO_3^-) is gradually reduced to nitrous oxide
40 (N_2O) and dinitrogen (N_2) (Zaman *et al.*, 2012); it is a major pathway of nitrogen (N) loss in

41 terrestrial ecosystems. N₂O emissions contribute to global warming and stratospheric ozone
42 depletion whereas N₂ losses decrease nitrogen use efficiency (NUE) in croplands and grasslands
43 (Bouwman *et al.*, 2013). The N loss through soil denitrification from terrestrial ecosystems was
44 estimated to be 105-185 Tg N yr⁻¹ (Tiedje, 1988) and 166 Tg N yr⁻¹ (Scheer *et al.* (2020), with
45 around 66-87 Tg N yr⁻¹ in global croplands (Hofstra and Bouwman, 2005; Seitzinger *et al.*, 2006)
46 and 5.6 Tg N yr⁻¹ in temperate grasslands (Saggar *et al.*, 2013). N₂ represents a substantial N loss
47 accounting for up to 85% of total denitrification (year 2000) (Bouwman *et al.*, 2013) but it is often
48 overlooked and poorly studied as N₂ is non-reactive (Almaraz *et al.*, 2020). The quantification of
49 N₂ emissions from terrestrial ecosystems remains challenging because of the high background
50 atmospheric N₂ concentration (Zaman *et al.*, 2012; Saggar *et al.*, 2013). Many empirical and
51 process-based models were developed to estimate N₂O and N₂ emissions from denitrification
52 based on a fixed N₂O to N₂ ratio (NOE model) (Hénault *et al.*, 2005) or combined with functions
53 of soil properties (e.g., APSIM and DayCent model) (Del Grosso *et al.*, 2000; Keating *et al.*, 2003;
54 Stehfest and Muller, 2004). However, the N₂O and N₂ emissions from soil denitrification showed
55 a large spatial and temporal heterogeneity at a global scale (Butterbach-Bahl and Dannenmann,
56 2011). Therefore, a better understanding of the N₂O/(N₂O+N₂) ratio and its driving factors could
57 improve the estimation of denitrification in earth system models (Almaraz *et al.*, 2020).

58 Soil denitrification and the emissions of its end-products (N₂O and N₂) are regulated by soil and
59 environmental factors. For example, soil NO₃⁻ availability affects the denitrification rate (Abbasi
60 and Adams, 1999; Senbayram *et al.*, 2019). Higher carbon (C) availability could increase the
61 denitrification rate but decrease the N₂O/N₂ ratio (Clough *et al.*, 1998; Gillam *et al.*, 2008). The
62 effect of soil pH on denitrification is controversial. It is generally accepted that acidic soil has a
63 lower soil denitrification rate (Sun *et al.*, 2012) and higher N₂O/(N₂O+N₂) ratio (Zaman *et al.*,

64 2007; Zaman and Nguyen, 2010). Soil pH can also indirectly affect denitrification because
65 nitrification is inhibited in acidic soils and subsequently less NO_3^- is available for denitrification
66 (Tiedje, 1988). On the contrary, Šimek *et al.* (2000) found no significant correlation between soil
67 pH and denitrifying enzyme activity. Soil oxygen concentration, water content and rainfall are
68 other important factors as anaerobic conditions favour denitrification (De Klein and Van
69 Logtestijn, 1996; Ellis *et al.*, 1998; Rudaz *et al.*, 1999; Hefting *et al.*, 2003; Saggar *et al.*, 2004).
70 Generally, soil temperature is positively related to soil denitrification rate and associated N_2O
71 emissions (Knowles, 1982; Ryden, 1983). However, some studies demonstrated that N_2O
72 emissions may decrease with increasing temperature, because elevated temperature may enhance
73 anaerobiosis and decrease the $\text{N}_2\text{O}/\text{N}_2$ ratio (Butterbach-Bahl and Dannenmann, 2011). These
74 inconsistencies highlight the need of a comprehensive assessment to identify the important drivers
75 of soil denitrification rate and its end-products.

76 Mitigation strategies have been widely investigated and adopted to lower soil denitrification and
77 increase NUE. Optimizing N application rate could reduce the excess N that is subjected to
78 denitrification (Morley *et al.*, 2014; Lai and Denton, 2018; Senbayram *et al.*, 2019). The
79 application of soil amendments e.g., lime (McMillan *et al.*, 2016) and biochar (Cayuela *et al.*,
80 2013) generally raised soil pH and increased the activities of N_2O reductase that might
81 subsequently decrease N_2O emissions from denitrification. Reduced crop residue retention
82 decreases organic C input for soil denitrifiers (Chintala *et al.*, 2015; Sun *et al.*, 2018) but may
83 reduce the potential of C sequestration and affect crop yield (Xia *et al.*, 2018). Avoiding excessive
84 irrigation could effectively maintain oxygen supply in the soil and lower denitrification (Huang *et*
85 *al.*, 2015). The application of nitrification inhibitors can reduce the NO_3^- availability for
86 denitrification by inhibiting nitrification without impairing crop yields (McGeough *et al.*, 2012;

87 Wang *et al.*, 2017). A systematic synthesis of mitigation strategies for denitrification and N₂ is
88 vital for improving global fertilizer NUE and environmental quality.

89 In this study, we compiled a comprehensive database based on peer-reviewed studies worldwide.
90 We attempted to 1) summarize and quantify soil denitrification rate, N₂ emissions and the
91 N₂O/(N₂O+N₂) ratio across different land use systems and climatic zones; 2) quantify the
92 relationships between soil/environmental factors and soil denitrification rate, N₂ emissions and the
93 N₂O/(N₂O+N₂) ratio; and 3) evaluate the effects of mitigation strategies on soil denitrification rate
94 and N₂ production.

95 **2 Data and Methods**

96 **2.1 Database compilation**

97 An extensive keyword search was conducted from Web of Science (ISI), CAB Abstracts (ISI) and
98 Google Scholar between 1978 and 2019. The keywords used for searching include the
99 combinations of denitrification, N₂/dinitrogen, nitrogen (N) application, mitigation strategy,
100 management practices, fertilizer type, soil amendment and inhibitor, N₂O/(N₂O+N₂) ratio. The
101 database was also cross-checked with the studies included in recent key review papers of
102 denitrification by Wang *et al.* (2018) and Almaraz *et al.* (2020). These papers did not examine the
103 aspects of land use types or mitigation strategies of soil denitrification and associated gaseous
104 losses. Literature included in our database fulfilled the following selection criteria: a) soil
105 denitrification rate and its N₂O or N₂ emissions in the topsoil (0-20 cm) were specified; b)
106 experimental design or lab incubation conditions were given; c) studies were restricted to terrestrial
107 ecosystems. After data collection, a total of 3367 observations (1599 observations for soil
108 denitrification rate, 860 observations for soil N₂ emissions and 908 observations for the
109 N₂O/(N₂O+N₂) ratio from soil denitrification) were included in the database.

110 In the database, geographic coordinates (latitude and longitude) of the study sites, environmental
 111 conditions (mean annual temperature [MAT] and mean annual precipitation [MAP]), soil
 112 physicochemical properties (e.g., soil texture, clay content, soil water filled pore space (WFPS),
 113 soil temperature under incubation condition, soil pH, soil total nitrogen (TN) and organic carbon
 114 (SOC) content, soil C/N ratio, NH_4^+ and NO_3^- concentrations at the beginning of the experiment,
 115 etc.), and management practices (N application rate and farming practices) were extracted. This
 116 database was used for conducting linear mixed-effect models (section 3.2) and a meta-analysis
 117 (section 3.3). To decrease the outliers' impact and increase the normality, some data were natural
 118 log transformed when necessary for statistical analysis.

119 The database covered the dominant vegetation types (e.g., upland fields, paddy fields, grasslands,
 120 forests and wetlands). Overall, these sites spanned from 123.27°W to 176.07°E and from 42.97°S
 121 to 60.62°N (Figure 1). These sites were classified into four major climatic zones according to
 122 Köppen Climate Classification (tropical, dry, temperate, and continental climates).

123 **2.2 Data analyses**

124 We calculated the emission factor of denitrification (EF_D) from field experiments conducted for at
 125 least a cropping season using the following equation:

$$126 \quad EF_D(\%) = \left(\frac{\text{cumulative denitrification N loss } (\text{N}_2\text{O}+\text{N}_2)_{\text{treatment}} - \text{cumulative denitrification N loss } (\text{N}_2\text{O}+\text{N}_2)_{\text{control}} (\text{kg N ha}^{-1})}{\text{N fertilizer/manure applied } (\text{kg N ha}^{-1})} \right) * 100 (\%)$$

127(1)

128 We then used linear mixed-effect models to explore the relationships between soil denitrification
 129 rate, soil N_2 emissions and the $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ ratio from denitrification with soil and
 130 environmental properties:

$$131 \quad \ln y = \alpha + \beta x + T_{\text{study}} + \varepsilon \quad (2)$$

132 Where y is soil denitrification rate and should be natural log transformed to satisfy the assumption
133 of normality in the context of the model, soil N_2 emissions or the $N_2O/(N_2O+N_2)$ ratio from
134 denitrification. α , β and ε are the intercept, slope and random error, respectively; x is the soil
135 WFPS, soil O_2 concentration, SOC, C/N ratio, NO_3^- concentration, soil temperature, soil mineral
136 N content, soil pH, N application rate or latitude. T is the random effect factor. We considered
137 ‘study’ as a random effect to reflect the non-independence among observations within the same
138 experiment. The linear mixed-effect model was performed using *lme4* package (Bates *et al.*, 2014)
139 and *lmerTest* package (Kuznetsova *et al.*, 2017). The average and median soil denitrification rate,
140 EF_D and $N_2O/(N_2O+N_2)$ ratio from denitrification were calculated. Tukey HSD test was performed
141 across land uses and climatic zones by *agricolae* package. (Mendiburu, 2014). These analyses
142 were conducted in R (RStudio, 2020).

143 We also used paired observations to perform a meta-analysis to examine the effects of mitigation
144 strategies on denitrification and N_2 emissions using our database. For N application, we used zero
145 or the lowest N as the control and the other N application rates as treatments. For fertilizer type,
146 we considered urea, a widely used fertilizer, as the control and other fertilizer types as treatments.
147 Fertilizer types were sub-divided into organic fertilizers (animal manure and solid waste),
148 ammonium-based fertilizers, nitrate-based fertilizers and NH_4NO_3 fertilizer. For management
149 practices, soil amendment (biochar, zeolite and lime) or the use of nitrification inhibitor was
150 compared to N fertilization only. We also considered no tillage, no irrigation, residue removal,
151 single fertilization and surface application of fertilizers as controls, and compared them with their
152 corresponding treatments: tillage, irrigation, residue retention, split fertilization and incorporation
153 of fertilizers.

154 Effect sizes in meta-analysis were weighed by the number of replicates in a study (Lam *et al.*,
155 2012) to avoid extreme weights:

$$156 \text{ Weight} = (n_c \times n_T) / (n_c + n_T) \quad (3)$$

157 Where n_c and n_T are the number of replicates of the control and treatment, respectively.

158 The response ratio r is represented by the natural log and used as a metric for soil denitrification
159 rate and N_2 emissions in response to management practices (Hedges *et al.*, 1999):

$$160 \ln r = \ln \left(\frac{\bar{x}^T}{\bar{x}^C} \right) \quad (4)$$

161 where \bar{x}^T and \bar{x}^C are the mean values of the treatment observation and the control observation,
162 respectively. Results of meta-analysis are reported as the percentage change of soil denitrification
163 and N_2 emissions under treatment effects $((r-1) \times 100)$. Fixed-effect meta-analysis with 4999
164 iterations bootstrapping was conducted to generate the mean effect size and the 95% confidence
165 intervals (CIs) by MetaWin version 2.1 (Rosenberg *et al.*, 2000). The effects of mitigation
166 strategies were considered significant if the 95% CIs did not overlap with zero.

167 **3 Results**

168 **3.1 Summary of soil denitrification and N_2 emissions studies**

169 The summarized data from 648 field observations suggested a mean daily loss of $0.25 \text{ kg N ha}^{-1}$
170 (median value of $0.06 \text{ kg N ha}^{-1}$) through soil denitrification (Figure 2). Soil denitrification rate
171 was the highest in wetlands with an average of $0.89 \text{ kg N ha}^{-1} \text{ d}^{-1}$ followed by paddy fields (0.62
172 $\text{kg N ha}^{-1} \text{ d}^{-1}$), while upland fields had a lower rate of $0.11 \text{ kg N ha}^{-1} \text{ d}^{-1}$. In terms of climatic zones,
173 the highest denitrification rate with an average of $0.83 \text{ kg N ha}^{-1} \text{ d}^{-1}$ was found in tropical areas
174 while the lowest rate ($0.11 \text{ kg N ha}^{-1} \text{ d}^{-1}$) in continental areas. The overall EF_D was 4.8% (median
175 value of 2.6%) (Figure 3). Paddy fields had the highest EF_D with an average of 27%, which was

176 significantly higher than grassland and upland fields (4.7% and 4.1%, respectively). Across
177 climatic zones, temperate regions had the highest mean EF_D (5.2 %), followed by continental and
178 dry areas (3.2% and 1.9%, respectively).

179 Overall, the mean $N_2O/(N_2O+N_2)$ ratio was 0.33 (Figure 4). The $N_2O/(N_2O+N_2)$ ratio across
180 different ecosystems followed the order of grassland (0.37) > wetland (0.36) > upland fields (0.35)
181 > paddy field (0.23) > forest (0.12), and that across climatic regions the order of continental (0.38)
182 > temperate (0.35) > dry (0.25) > tropical (0.20).

183 **3.2 Bivariate relationships of soil denitrification rate, N_2 emissions and $N_2O/(N_2O+N_2)$ with** 184 **soil and environmental properties**

185 Soil denitrification rate was significantly increased with soil WFPS ($p < 0.001$; Figure 5a) but
186 decreased with increasing O_2 concentration ($p < 0.001$; Figure 5b). Soil denitrification rate was
187 positively related to soil NO_3^- content ($p < 0.05$; Figure 5c) and mineral N content ($p < 0.05$; Figure
188 5d). The relationship between soil denitrification and soil pH was not significant (Figure 5e). Soil
189 temperature was positively correlated to soil denitrification rate ($p < 0.001$, Figure 5f).

190 Soil N_2 emissions from denitrification significantly increased from low to high latitude ($p < 0.05$;
191 Figure 6a). Soil mineral N and WFPS were positively related to soil N_2 emissions ($p < 0.05$ and
192 $p < 0.001$, respectively; Figure 6b, c). N_2 emissions decreased significantly with increased O_2
193 concentration ($p < 0.05$; Figure 6d).

194 The $N_2O/(N_2O+N_2)$ ratio was negatively related to soil pH ($p < 0.05$; Figure 7a) and WFPS ($p < 0.01$,
195 Figure 7b). The soil C/N ratio and organic C contents were also negatively related to the
196 $N_2O/(N_2O+N_2)$ ratio ($p < 0.05$; Figure 7d, f). However, the $N_2O/(N_2O+N_2)$ ratio was positively
197 related to soil O_2 concentration ($p < 0.01$; Figure 7c).

198 **3.3 The effect of management practices on soil denitrification rate and N₂ production**

199 Increasing N application rate significantly increased soil denitrification rate by 219% (Figure 8a)
200 and N₂ emissions by 204% (Figure 8b). Under the same N application rate, compared to urea, other
201 types of fertilizer led to higher soil denitrification rate by 77% (Figure 8a). Among these fertilizer
202 types, the application of NO₃⁻-based fertilizer produced the highest increase in soil denitrification
203 rate (199%) (Figure 8a), whereas applying NH₄-based fertilizer significantly reduced N₂ emissions
204 by 56% (Figure 8b). Lime application significantly increased soil denitrification rate and N₂
205 emissions by 52% and 48%, respectively (Figure 8a, b), whereas biochar application reduced soil
206 denitrification rate by 38% but had no significant effect on N₂ emissions. The application of zeolite
207 had no significant effects on soil denitrification or N₂ production. Residue retention and irrigation
208 significantly increased soil denitrification rate (144% and 75%, respectively) and N₂ emissions
209 (226% and 102%, respectively) (Figure 8a, b). Tillage, split application and fertilizer incorporation
210 had no significant effects on soil denitrification rate or N₂ emissions (Figure 8a, b). Overall,
211 nitrification inhibitor application significantly reduced soil denitrification rate and N₂ emissions
212 by 41% and 30%, respectively (Figure 8a, b). 3,4-Dimethylpyrazole phosphate (DMPP) was the
213 most effective inhibitor in reducing denitrification rate (71%) and N₂ emissions (68%).
214 Dicyandiamide (DCD) reduced soil denitrification rate but had no significant effect on N₂
215 emissions. 2-Chloro-6-(trichloromethyl) pyridine (Nitrapyrin) decreased N₂ emissions by 15%.

216 **4 Discussion**

217 **4.1 Denitrification is a key N loss pathway globally**

218 Denitrification occurs in a wide range of terrestrial ecosystems. Typically, denitrification requires
219 an anoxic environment with readily available soil NO₃⁻ and organic C, so fertilized and/or irrigated
220 paddy fields and grasslands located in humid areas had higher denitrification rates (Figure 2).

221 Moreover, anaerobic microsites within soil aggregates can produce hot-spots and hot moments of
222 denitrification activity, resulting in significant denitrification from apparently well-drained soils
223 (Scheer *et al.*, 2020), such as in the croplands and grasslands in dry climatic areas. The average
224 EF_D calculated in our study was 4.8% and could be up to 41.7% in paddy fields and grasslands in
225 temperate areas (Figure 3). This indicated that better management strategies should be adopted
226 because N loss via denitrification could decrease NUE and plant productivity.

227 The $N_2O/(N_2O+N_2)$ ratio varied greatly across land use types and climatic zones with a mean value
228 of 0.33, which implies that N_2 emissions dominated the end-products of denitrification. The
229 $N_2O/(N_2O+N_2)$ ratio in denitrification was used to estimate N_2 emissions in process-based models.
230 These models generally assume the ratio is a fixed value (Hénault *et al.*, 2005) or determined by a
231 function based on soil properties such as soil water condition and soil NO_3^- content (Del Grosso
232 *et al.*, 2000; Stehfest and Muller, 2004; Li *et al.*, 2007). In this regard, the wide range of
233 $N_2O/(N_2O+N_2)$ ratio observed in this study suggests that the estimation of N_2 emissions in process-
234 based models is highly uncertain. In fact, the $N_2O/(N_2O+N_2)$ ratio adopted in process-based models
235 was derived from limited datasets and the relationships between N_2 emission and its key drivers
236 might not have been well captured in these models.

237 **4.2 Key factors of soil denitrification rate, N_2 emissions and $N_2O/(N_2O+N_2)$ ratio**

238 We found that N loss via denitrification could be substantial and varied greatly with edaphic and
239 environmental conditions. These results confirm the traditional conceptual frameworks laid out by
240 Tiedje (1988) and Robertson (1989). Meanwhile, a better understanding of the driving factors of
241 denitrification and its end products is vital for developing effective management strategies that
242 mitigate N_2O and N_2 losses and improve NUE.

243 Soil NO_3^- is the primary N substrate for soil denitrifying bacteria. We found that soil NO_3^- content
244 was positively related to denitrification rate, which has been widely reported (Zaman *et al.*, 2007;
245 Senbayram *et al.*, 2012). According to our database, when soil NO_3^- content reached a high level
246 (80 mg N kg^{-1}), a higher $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ ratio (>0.5) was observed in highly fertilized soils such
247 as croplands and grasslands. This could be attributed to the suppression of the activity of N_2O
248 reductase, the enzyme responsible for reducing N_2O to N_2 (Senbayram *et al.*, 2019), resulting in
249 incomplete denitrification and higher $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ ratio (Blackmer and Bremner, 1978; Stevens
250 and Laughlin, 1998).

251 With decreased WFPS, the synthesis of denitrifying enzymes and N_2O reductase is relatively
252 inhibited; thus, denitrification is reduced (Hwang and Hanaki, 2000). Our database indicated that
253 when WFPS was over 72%, more N_2 than N_2O was emitted through denitrification, thereby
254 decreasing $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ ratio. The activity of N_2O reductase was decreased with increased soil
255 O_2 concentration (Friedl *et al.*, 2016). At high soil water content, the limited O_2 availability in the
256 soil resulted in anaerobic conditions. Subsequently, N_2O reductase capacity was upregulated,
257 leading to a lower $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ ratio (Figure 7c).

258 We found that denitrification occurred over a wide range of soil temperatures ($2\text{-}45^\circ\text{C}$) and was
259 positively related to soil temperature (Figure 5f). Soil respiration increased with soil temperature,
260 resulting in O_2 depletion and anaerobic conditions. This promoted the activity of denitrifiers and
261 denitrification (Lai and Denton, 2018).

262 Soil pH regulates denitrification and its end products (Dannenmann *et al.*, 2008; Sun *et al.*, 2012).
263 N_2O reductase was less active under low pH (Liu *et al.*, 2010). At a reduced soil pH, denitrification
264 may liberate more N_2O and subsequently increase the ratio of $\text{N}_2\text{O}/(\text{N}_2\text{O}+\text{N}_2)$ (Simek and Cooper,
265 2002; Cuhel *et al.*, 2010; Qu *et al.*, 2014). However, the relationship between denitrification and

266 soil pH was not significant in this study (Figure 5e). This might be attributed to the confounding
267 effects of other factors such as the application of N fertilizers and organic amendments under
268 aerobic conditions in upland fields and grasslands. Under anaerobic conditions (paddy fields and
269 wetlands) soil pH was positively correlated with denitrification (Figure S4).

270 We found that for a soil with a higher C/N ratio (>14), more N_2O was reduced to N_2 , decreasing
271 the $N_2O/(N_2O+N_2)$ ratio from denitrification (Figure 7d). This is because higher soil C/N ratio
272 promoted denitrifying population and the diffusion rate of soil NO_3^- into denitrifying microsites
273 (Saggar *et al.*, 2013). Moreover, soil organic C was highly related to the ratio of N_2O to total
274 denitrification (Figure 7f). More available C could promote the growth of soil microorganisms and
275 increase N_2O reductase in the soil, which could reduce the $N_2O/(N_2O+N_2)$ ratio from
276 denitrification. However, the effect of soil organic C on $N_2O/(N_2O+N_2)$ can be outweighed by
277 other factors, such as soil NO_3^- content (Weier *et al.*, 1993).

278 **4.3 Management practices to mitigate soil denitrification and N_2 emissions**

279 Our meta-analysis showed that optimizing N application rate to match plant N demand and
280 avoiding excessive NO_3^- in the soil can effectively reduce denitrification and N_2 emissions (Figure
281 S1d). The type of N fertilizers can also impact denitrification and N_2 emissions. Compared to urea,
282 NO_3^- based fertilizers and organic fertilizers significantly increased denitrification by 77% (Figure
283 8) under the same application rate. Nitrate-based fertilizers provide more NO_3^- compared to urea,
284 which is the key substrate for denitrification. We found that soil NO_3^- content was significantly
285 correlated with soil denitrification rate and N_2 emissions (Figure 5c, 6e). Our analysis also
286 indicated that the application of urea/ammonium-based fertilizers could reduce N_2 emissions
287 compared to nitrate-based or organic fertilizers. When nitrate-based fertilizers are applied, more
288 NO_3^- is available for denitrification and subsequent gaseous losses (Wang *et al.*, 2018). Organic

289 fertilizers like livestock manure, increased denitrification by providing the energy source (readily
290 available C) for denitrifiers and aggravate anaerobic conditions through its decomposition (Figure
291 9) (Estavillo *et al.*, 1994; Mogge *et al.*, 1998; Barton *et al.*, 1999).

292 Managing crop residue properly is important to regulate denitrification and N₂ emissions without
293 impairing soil fertility and crop yields. Our results showed that residue retention could increase
294 denitrification and N₂ emissions by 144% and 226%, respectively (Figure 8), because it can
295 increase C availability for denitrifiers and promote subsequent denitrification (Garcia-Montiel *et*
296 *al.*, 2003). In addition, crop residue decomposition consumes O₂ thereby inducing higher
297 denitrification and N₂ emissions (Clough *et al.*, 1998; Gillam *et al.*, 2008) (Figure 9). It is worth
298 nothing that the effect of residue retention on denitrification and N₂ emissions is highly related to
299 residue quality. Incorporating crop residues with low C/N ratios would promote denitrification by
300 providing sufficient N for soil microbial growth and proliferation (Xia *et al.*, 2018). However, the
301 application of crop residue with higher C/N ratios (e.g., wheat straw and switchgrass) could reduce
302 denitrification by promoting soil microbial N immobilization (Sun *et al.*, 2018).

303 Irrigation could temporarily increase soil water content and develop an anaerobic zone that favours
304 denitrification especially for fine-textured soils (De Klein and Van Logtestijn, 1996; Zaman *et al.*,
305 2012; Saggari *et al.*, 2013) (Figure 9). In this regard, advanced irrigation techniques (e.g., drip
306 irrigation) should be adopted to reduce denitrification and associated N₂ emissions (Barakat *et al.*,
307 2016).

308 Biochar application effectively reduced soil denitrification rate by 38% (Figure 8a), because it
309 promoted the chemical affinity of inorganic N substrates (Cayuela *et al.*, 2013; Chintala *et al.*,
310 2015). However, N₂ emissions overall were not significantly affected by biochar application
311 (Figure 8b), likely because biochars have diverse characteristics e.g., pH and C/N ratio, and may

312 exert contrasting effects on N₂ emissions (Malghani *et al.*, 2018). Lime is often applied in pastures
313 and wetlands to decrease total N₂O emissions (Saggar *et al.*, 2013) but may increase soil
314 denitrification rate and N₂ emissions (Simek and Cooper, 2002). Liming can also increase soil pH
315 and subsequently enhance the activity of N₂O reductase, which reduces N₂O to N₂ in acidic soils.
316 Nitrification inhibitors delay the conversion of NH₄⁺ to NO₃⁻ via nitrification (Zaman *et al.*, 2012)
317 (Figure 9). This delay maintains the applied N fertilizer/animal manure in the form of NH₄⁺
318 limiting NO₃⁻ availability for denitrification and decreases N₂O and N₂ emissions (McGeough *et*
319 *al.*, 2012; Maris *et al.*, 2015; Friedl *et al.*, 2017). However, nitrification inhibitors may increase N
320 loss via NH₃ volatilization (Pan *et al.*, 2016; Lam *et al.*, 2017; Xia *et al.*, 2017; Lam *et al.*, 2018).
321 Therefore, additional knowledge-based N managements (e.g., fertilizer deep placement) should be
322 adopted simultaneously with nitrification inhibitors to reduce the overall N losses (Xia *et al.*,
323 2020).

324 Many studies have focused on mitigation strategies to reduce potent greenhouse gas N₂O emissions
325 and how to facilitate N₂O reduction to N₂. However, from the perspective of N use efficiency, N
326 loss via N₂ should be minimized. Management practices that can reduce both denitrification and
327 N₂ emissions should be recommended considering the trade-off between N₂O mitigation and N use
328 efficiency improvement. Our meta-analysis suggests that reduced N application rate, use of
329 ammonium-based fertilizers, reduced residue retention, biochar amendment and nitrification
330 inhibitors, and improved irrigation techniques such as drip irrigation could effectively reduce
331 denitrification and N₂ emissions.

332 **5 Uncertainty**

333 We are aware that the number of observations included in the database varies largely across land
334 uses; more relevant studies should be conducted in different ecosystems. Moreover, the acetylene

335 inhibition technique (AIT) has been widely used but may underestimate denitrification rate (Wang
336 and Yan, 2016) under both field and laboratory conditions (Figure S5) mainly owing to the
337 inhibition of nitrification (Groffman *et al.*, 2006; Qin *et al.*, 2013). Previous studies demonstrated
338 that AIT may underestimate denitrification by 4-10 times compared to ¹⁵N tracer method or gas-
339 flow-soil-core techniques when applied to the same soils (Watts and Seitzinger, 2000; Lindau *et*
340 *al.*, 2011; Sgouridis *et al.*, 2016). Although ¹⁵N tracer method or gas flow core techniques could
341 reliably estimate denitrification rate (Groffman *et al.*, 2006), they are not widely adopted, as
342 evidenced by the number of observations in our database (¹⁵N-gas flux method: n=268; gas-flow
343 (helium or Ar) method: n=131; AIT: n=1200). Such bias in the observation number among
344 different methods might have caused uncertainties in quantifying soil denitrification rate in this
345 study. Besides, some studies that used Nitrogen-Free Air Recirculation Method (N-FARM) to
346 measure the denitrification rate (Burgin and Groffman, 2012) may overestimate the N₂O from
347 denitrification because it cannot distinguish the N₂O produced from denitrification and that from
348 nitrification. Therefore, more studies using advanced techniques should be conducted. We are also
349 aware that NO emissions are a product of denitrification and some studies applied stable isotope
350 models (Houlton *et al.*, 2006) to estimate NO emission from denitrification. We only identified
351 N₂O and N₂ emissions from denitrification owing to the limited studies on NO/N₂O/N₂ ratio.

352 **6 Conclusions**

353 We compiled a global database on denitrification rate and its N₂O and N₂ emissions. We found
354 that N loss through denitrification varied greatly across land uses and climatic regions. The average
355 EF_D was 4.8%. The wide range of N₂O/(N₂O+N₂) demonstrated that the adoption of a fixed ratio
356 in some process-based models for estimating N₂ emissions from denitrification is not suitable. We
357 found that N₂ loss accounted for 67% of total denitrification. N loss as N₂, although harmless to

358 the environment, deserves more attention from the perspective of improving N use efficiency.
359 Denitrification and its N₂O and N₂ emissions are highly dependent on soil properties, e.g., soil
360 mineral N, soil water, temperature and oxygen conditions. We further examined the potential of
361 mitigation strategies in decreasing denitrification and N₂ emissions. Specifically, optimized N
362 input, the use of ammonium-based fertilizers, biochar amendment, use of nitrification inhibitors,
363 and advanced irrigation technique could effectively decrease denitrification and N₂ emissions.

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369 **References**

- 370 Abbasi, M.K., Adams, W.A., 1999. Assessment of the contribution of denitrification to N losses
371 from compacted grassland soil by NO₃⁻ disappearance and N₂O production during anaerobic
372 incubation. *Can. J. Soil Sci.* 79, 57-64.
- 373 Almaraz, M., Wong, M.Y., Yang, W.H., 2020. Looking back to look ahead: a vision for soil
374 denitrification research. *Ecology* 101, 02917.
- 375 Barakat, M., Cheviron, B., Angulo-Jaramillo, R., 2016. Influence of the irrigation technique and
376 strategies on the nitrogen cycle and budget: A review. *Agric. Water Manag* 178, 225-238.
- 377 Barton, L., McLay, C., Schipper, L., Smith, C., 1999. Annual denitrification rates in agricultural
378 and forest soils: a review. *Soil Res.* 37, 1073-1094.

379 Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using
380 Eigen and S4. R package version 1.1-7.

381 Blackmer, A., Bremner, J., 1978. Inhibitory effect of nitrate on reduction of N₂O to N₂ by soil
382 microorganisms. *Soil Biol. Biochem.* 10, 187-191.

383 Bouwman, A., Beusen, A., Griffioen, J., Van Groenigen, J., Hefting, M., Oenema, O., Van
384 Puijenbroek, P., Seitzinger, S., Slomp, C., Stehfest, E., 2013. Global trends and uncertainties in
385 terrestrial denitrification and N₂O emissions. *Philos. Trans. R. Soc. B* 368, 20130112.

386 Burgin, A.J., Groffman, P.M., 2012. Soil O₂ controls denitrification rates and N₂O yield in a
387 riparian wetland. *J. Geophys. Res. Biogeosci.* 117.

388 Butterbach-Bahl, K., Dannenmann, M., 2011. Denitrification and associated soil N₂O emissions
389 due to agricultural activities in a changing climate. *Curr Opin Environ Sustain.* 3, 389-395.

390 Cayuela, M.L., Sánchez-Monedero, M.A., Roig, A., Hanley, K., Enders, A., Lehmann, J., 2013.
391 Biochar and denitrification in soils: when, how much and why does biochar reduce N₂O
392 emissions? *Sci. Rep.* 3.

393 Chintala, R., Owen, R.K., Schumacher, T.E., Spokas, K.A., McDonald, L.M., Kumar, S., Clay,
394 D.E., Malo, D.D., Bleakley, B., 2015. Denitrification kinetics in biomass-and biochar-amended
395 soils of different landscape positions. *Environ. Sci. Pollut. Res.* 22, 5152-5163.

396 Clough, T.J., Jarvis, S.C., Dixon, E.R., Stevens, R.J., Laughlin, R.J., Hatch, D.J., 1998. Carbon
397 induced subsoil denitrification of ¹⁵N-labelled nitrate in 1 m deep soil columns. *Soil Biol.*
398 *Biochem.* 31, 31-41.

399 Cuhel, J., Simek, M., Laughlin, R.J., Bru, D., Cheneby, D., Watson, C.J., Philippot, L., 2010.
400 Insights into the effect of soil pH on N₂O and N₂ emissions and denitrifier community size and
401 activity. *Appl. Environ. Microbiol.* 76, 1870-1878.

402 Dannenmann, M., Butterbach-Bahl, K., Gasche, R., Willibald, G., Papen, H., 2008. Dinitrogen
403 emissions and the N₂: N₂O emission ratio of a Rendzic Leptosol as influenced by pH and forest
404 thinning. *Soil Biol. Biochem.* 40, 2317-2323.

405 De Klein, C., Van Logtestijn, R., 1996. Denitrification in grassland soils in the Netherlands in
406 relation to irrigation, N-application rate, soil water content and soil temperature. *Soil Biol.*
407 *Biochem.* 28, 231-237.

408 Del Grosso, S.J., Parton, W.J., Mosier, A.R., Ojima, D.S., Kulmala, A.E., Phongpan, S., 2000.
409 General model for N₂O and N₂ gas emissions from soils due to denitrification. *Glob.*
410 *Biogeochem. Cycles.* 14, 1045-1060.

411 Ellis, S., Yamulki, S., Dixon, E., Harrison, R., Jarvis, S., 1998. Denitrification and N₂O
412 emissions from a UK pasture soil following the early spring application of cattle slurry and
413 mineral fertiliser. *Plant Soil* 202, 15-25.

414 Estavillo, J., Rodriguez, M., Domingo, M., Munoz-Rueda, A., Gonzalez-Murua, C., 1994.
415 Denitrification losses from a natural grassland in the Basque Country under organic and
416 inorganic fertilization. *Plant Soil* 162, 19-29.

417 Friedl, J., Scheer, C., Rowlings, D.W., McIntosh, H.V., Strazzabosco, A., Warner, D.I., Grace,
418 P.R., 2016. Denitrification losses from an intensively managed sub-tropical pasture—Impact of
419 soil moisture on the partitioning of N₂ and N₂O emissions. *Soil Biol. Biochem.* 92, 58-66.

420 Friedl, J., Scheer, C., Rowlings, D.W., Mumford, M.T., Grace, P.R., 2017. The nitrification
421 inhibitor DMPP (3,4-dimethylpyrazole phosphate) reduces N₂ emissions from intensively
422 managed pastures in subtropical Australia. *Soil Biol. Biochem.* 108, 55-64.

423 Garcia-Montiel, D., Melillo, J., Steudler, P., Cerri, C., Piccolo, M., 2003. Carbon limitations to
424 nitrous oxide emissions in a humid tropical forest of the Brazilian Amazon. *Biol. Fertil. Soils.*
425 38, 267-272.

426 Gillam, K.M., Zebarth, B.J., Burton, D.L., 2008. Nitrous oxide emissions from denitrification
427 and the partitioning of gaseous losses as affected by nitrate and carbon addition and soil aeration.
428 *Can. J. Soil Sci.* 88, 133-143.

429 Groffman, P.M., Altabet, M.A., Böhlke, J., Butterbach-Bahl, K., David, M.B., Firestone, M.K.,
430 Giblin, A.E., Kana, T.M., Nielsen, L.P., Voytek, M.A., 2006. Methods for measuring
431 denitrification: diverse approaches to a difficult problem. *Ecol. Appl.* 16, 2091-2122.

432 Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in
433 experimental ecology. *Ecology* 80, 1150-1156.

434 Hefting, M.M., Bobbink, R., de Caluwe, H., 2003. Nitrous oxide emission and denitrification in
435 chronically nitrate-loaded riparian buffer zones. *J. Environ. Qual.* 32, 1194-1203.

436 Hénault, C., Bizouard, F., Laville, P., Gabrielle, B., Nicoullaud, B., Germon, J., Cellier, P., 2005.
437 Predicting in situ soil N₂O emission using NOE algorithm and soil database. *Glob. Chang. Biol.*
438 11, 115-127.

439 Hofstra, N., Bouwman, A.F., 2005. Denitrification in agricultural soils: summarizing published
440 data and estimating global annual rates. *Nutr. Cycl. Agroecosystems.* 72, 267-278.

441 Houlton, B.Z., Sigman, D.M., Hedin, L.O., 2006. Isotopic evidence for large gaseous nitrogen
442 losses from tropical rainforests. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8745-8750.

443 Huang, P., Zhang, J., Zhu, A., Xin, X., Zhang, C., Ma, D., Yang, S., Mirza, Z., Wu, S., 2015.
444 Coupled water and nitrogen (N) management as a key strategy for the mitigation of gaseous N
445 losses in the Huang-Huai-Hai Plain. *Biol. Fertil. Soils.* 51, 333-342.

446 Hwang, S.J., Hanaki, K., 2000. Effects of oxygen concentration and moisture content of refuse
447 on nitrification, denitrification and nitrous oxide production. *Bioresour. Technol.* 71, 159-165.

448 Keating, B.A., Carberry, P.S., Hammer, G.L., Probert, M.E., Robertson, M.J., Holzworth, D.,
449 Huth, N.I., Hargreaves, J.N., Meinke, H., Hochman, Z., 2003. An overview of APSIM, a model
450 designed for farming systems simulation. *Eur. J. Agron.* 18, 267-288.

451 Knowles, R., 1982. Denitrification. *Microbiol. Rev.* 46, 43.

452 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H., 2017. lmerTest package: tests in linear
453 mixed effects models. *Journal of statistical software* 82, 1-26.

454 Lai, T.V., Denton, M.D., 2018. N₂O and N₂ emissions from denitrification respond differently to
455 temperature and nitrogen supply. *J. Soils Sediments.* 18, 1548-1557.

456 Lam, S.K., Chen, D., Norton, R., Armstrong, R., Mosier, A.R., 2012. Nitrogen dynamics in grain
457 crop and legume pasture systems under elevated atmospheric carbon dioxide concentration: A
458 meta-analysis. *Global Change Biol.* 18, 2853-2859.

459 Lam, S.K., Suter, H., Davies, R., Bai, M., Mosier, A.R., Sun, J., Chen, D., 2018. Direct and
460 indirect greenhouse gas emissions from two intensive vegetable farms applied with a nitrification
461 inhibitor. *Soil Biol. Biochem.* 116, 48-51.

462 Lam, S.K., Suter, H., Mosier, A.R., Chen, D., 2017. Using nitrification inhibitors to mitigate
463 agricultural N₂O emission: a double-edged sword? *Glob. Chang. Biol.* 23, 485-489.

464 Li, Y., White, R., Chen, D., Zhang, J., Li, B., Zhang, Y., Huang, Y., Edis, R., 2007. A spatially
465 referenced water and nitrogen management model (WNMM) for (irrigated) intensive cropping
466 systems in the North China Plain. *Ecol. Model.* 203, 395-423.

467 Lindau, C.W., Scaroni, A.E., Rivera-Monroy, V.H., Nyman, J.A., 2011. Comparison of $^{15}\text{N}_2$ flux
468 and acetylene inhibition denitrification methods in Atchafalaya River basin sediments. *J. Freshw.*
469 *Ecol.* 26, 337-344.

470 Liu, B., Mørkved, P.T., Frostegård, Å., Bakken, L.R., 2010. Denitrification gene pools,
471 transcription and kinetics of NO , N_2O and N_2 production as affected by soil pH. *FEMS*
472 *Microbiol. Ecol.* 72, 407-417.

473 Malghani, S., Kim, J., Lee, S.H., Yoo, G.Y., Kang, H., 2018. Application of two contrasting rice-
474 residue-based biochars triggered gaseous loss of nitrogen under denitrification-favoring
475 conditions: A short-term study based on acetylene inhibition technique. *Appl. Soil Ecol.* 127,
476 112-119.

477 Maris, S., Teira-Esmatges, M., Arbonés, A., Rufat, J., 2015. Effect of irrigation, nitrogen
478 application, and a nitrification inhibitor on nitrous oxide, carbon dioxide and methane emissions
479 from an olive (*Olea europaea* L.) orchard. *Sci. Total Environ.* 538, 966-978.

480 McGeough, K., Laughlin, R.J., Watson, C., Müller, C., Ernfors, M., Cahalan, E., Richards, K.G.,
481 2012. The effect of cattle slurry in combination with nitrate and the nitrification inhibitor
482 dicyandiamide on in situ nitrous oxide and dinitrogen emissions. *Biogeosciences* 9, 4909-4919.

483 McMillan, A.M.S., Pal, P., Phillips, R.L., Palmada, T., Berben, P.H., Jha, N., Sagar, S., Luo,
484 J.F., 2016. Can pH amendments in grazed pastures help reduce N_2O emissions from
485 denitrification? - The effects of liming and urine addition on the completion of denitrification in
486 fluvial and volcanic soils. *Soil Biol. Biochem.* 93, 90-104.

487 Mendiburu, F., 2014. Statistical Procedures for Agricultural Research. R package version 1.2-1.
488 IOP Publishing PhysicsWeb. <http://CRAN.R-project.org/package=agricolae>

489 Mogge, B., Kaiser, E.-A., Munch, J.-C., 1998. Nitrous oxide emissions and denitrification N-
490 losses from forest soils in the Bornhöved Lake region (Northern Germany). *Soil Biol. Biochem.*
491 30, 703-710.

492 Morley, N.J., Richardson, D.J., Baggs, E.M., 2014. Substrate induced denitrification over or
493 under estimates shifts in soil N₂/N₂O ratios. *PLoS One* 9.

494 Pan, Lam, Mosier, Luo, Chen, 2016. Ammonia volatilization from synthetic fertilizers and its
495 mitigation strategies: a global synthesis. *Agric. Ecosyst. Environ* 232, 283-289.

496 Qin, S., Yuan, H., Dong, W., Hu, C., Oenema, O., Zhang, Y., 2013. Relationship between soil
497 properties and the bias of N₂O reduction by acetylene inhibition technique for analyzing soil
498 denitrification potential. *Soil Biol. Biochem.* 66, 182-187.

499 Qu, Z., Wang, J.G., Almoy, T., Bakken, L.R., 2014. Excessive use of nitrogen in Chinese
500 agriculture results in high N₂O/(N₂O+N₂) product ratio of denitrification, primarily due to
501 acidification of the soils. *Glob. Change Biol.* 20, 1685-1698.

502 Robertson, G., 1989. Nitrification and denitrification in humid tropical ecosystems: potential
503 controls on nitrogen retention. *Mineral nutrients in tropical forest and savanna ecosystems* 9, 55-
504 69.

505 Rosenberg, M.S., Adams, D.C., Gurevitch, J.M., 2000. Statistical software for meta-analysis.
506 Version.

507 RStudio, 2020. RStudio: Integrated Development for R. RStudio, PBC. Boston, MA.

508 Rudaz, A., Wälti, E., Kyburz, G., Lehmann, P., Fuhrer, J., 1999. Temporal variation in N₂O and
509 N₂ fluxes from a permanent pasture in Switzerland in relation to management, soil water content
510 and soil temperature. *Agric. Ecosyst. Environ.* 73, 83-91.

511 Ryden, J., 1983. Denitrification loss from a grassland soil in the field receiving different rates of
512 nitrogen as ammonium nitrate. *Eur. J. Soil Sci.* 34, 355-365.

513 Sagggar, S., Andrew, R., Tate, K., Hedley, C., Rodda, N., Townsend, J., 2004. Modelling nitrous
514 oxide emissions from dairy-grazed pastures. *Nutr. Cycl. Agroecosystems.* 68, 243-255.

515 Sagggar, S., Jha, N., Deslippe, J., Bolan, N.S., Luo, J., Giltrap, D.L., Kim, D.G., Zaman, M.,
516 Tillman, R.W., 2013. Denitrification and $N_2O:N_2$ production in temperate grasslands: Processes,
517 measurements, modelling and mitigating negative impacts. *Sci. Total Environ.* 465, 173-195.

518 Scheer, C., Fuchs, K., Pelster, D.E., Butterbach-Bahl, K., 2020. Estimating global terrestrial
519 denitrification from measured $N_2O:(N_2O + N_2)$ product ratios. *Curr Opin Environ Sustain.* 47,
520 72-80.

521 Seitzinger, S., Harrison, J.A., Böhlke, J., Bouwman, A., Lowrance, R., Peterson, B., Tobias, C.,
522 Drecht, G.V., 2006. Denitrification across landscapes and waterscapes: a synthesis. *Ecol. Appl.*
523 16, 2064-2090.

524 Senbayram, M., Budai, A., Bol, R., Chadwick, D., Marton, L., Gündogan, R., Wu, D., 2019. Soil
525 NO_3^- level and O_2 availability are key factors in controlling N_2O reduction to N_2 following long-
526 term liming of an acidic sandy soil. *Soil Biol. Biochem.* 132, 165-173.

527 Senbayram, M., Chen, R., Budai, A., Bakken, L., Dittert, K., 2012. N_2O emission and the
528 $N_2O/(N_2O + N_2)$ product ratio of denitrification as controlled by available carbon substrates and
529 nitrate concentrations. *Agric. Ecosyst. Environ* 147, 4-12.

530 Sgouridis, F., Stott, A., Ullah, S., 2016. Application of the ^{15}N gas-flux method for measuring in
531 situ N_2 and N_2O fluxes due to denitrification in natural and semi-natural terrestrial ecosystems
532 and comparison with the acetylene inhibition technique. *Biogeosciences* 13, 1821-1835.

533 Simek, M., Cooper, J.E., 2002. The influence of soil pH on denitrification: progress towards the
534 understanding of this interaction over the last 50 years. *Eur. J. Soil Sci.* 53, 345-354.

535 Šimek, M., Cooper, J.E., Pícek, T., Šantrůčková, H., 2000. Denitrification in arable soils in
536 relation to their physico-chemical properties and fertilization practice. *Soil Biol. Biochem.* 32,
537 101-110.

538 Stehfest, E., Muller, C., 2004. Simulation of N₂O emissions from a urine-affected pasture in New
539 Zealand with the ecosystem model DayCent. *J. Geophys. Res. Atmos.* 109, D3.

540 Stevens, R.J., Laughlin, R.J., 1998. Measurement of nitrous oxide and di-nitrogen emissions
541 from agricultural soils. *Nutr. Cycl. Agroecosystems.* 52, 131-139.

542 Sun, P.P., Zhuge, Y.P., Zhang, J.B., Cai, Z.C., 2012. Soil pH was the main controlling factor of
543 the denitrification rates and N₂/N₂O emission ratios in forest and grassland soils along the
544 Northeast China Transect (NECT). *Soil Sci. Plant Nutr.* 58, 517-525.

545 Sun, Z.Y., Zheng, T.Y., Xin, J., Zheng, X.L., Hu, R.T., Subhan, F., Shao, H.B., 2018. Effects of
546 alkali-treated agricultural residues on nitrate removal and N₂O reduction of denitrification in
547 unsaturated soil. *J. Environ. Manage.* 214, 276-282.

548 Tiedje, J.M., 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium.
549 *Biol. Anaerob. Microorg.* 717, 179-244.

550 Wang, J., Chadwick, D.R., Cheng, Y., Yan, X., 2018. Global analysis of agricultural soil
551 denitrification in response to fertilizer nitrogen. *Sci. Total Environ.* 616-617, 908-917.

552 Wang, J.Y., Yan, X.Y., 2016. Denitrification in upland of China: Magnitude and influencing
553 factors. *J. Geophys. Res. Biogeosci.* 121, 3060-3071.

554 Wang, S.W., Shan, J., Xia, Y.Q., Tang, Q., Xia, L.L., Lin, J.H., Yan, X.Y., 2017. Different
555 effects of biochar and a nitrification inhibitor application on paddy soil denitrification: A field
556 experiment over two consecutive rice-growing seasons. *Sci. Total Environ.* 593, 347-356.

557 Watts, S.H., Seitzinger, S.P., 2000. Denitrification rates in organic and mineral soils from
558 riparian sites: a comparison of N₂ flux and acetylene inhibition methods. *Soil Biol. Biochem.* 32,
559 1383-1392.

560 Weier, K.L., Doran, J.W., Power, J.F., Walters, D.T., 1993. Denitrification and the
561 dinitrogen/nitrous oxide ratio as affected by soil water, available carbon and nitrate. *Soil Sci.*
562 *Soc. Am. J* 57, 66-72.

563 Xia, L., Lam, S.K., Chen, D., Wang, J., Tang, Q., Yan, X., 2017. Can knowledge-based N
564 management produce more staple grain with lower greenhouse gas emission and reactive
565 nitrogen pollution? A meta-analysis. *Glob. Change Biol.* 23, 1917-1925.

566 Xia, L., Lam, S.K., Wolf, B., Kiese, R., Chen, D., Butterbach-Bahl, K., 2018. Trade-offs
567 between soil carbon sequestration and reactive nitrogen losses under straw return in global
568 agroecosystems. *Glob. Change Biol.* 24, 5919-5932.

569 Xia, L., Li, X., Ma, Q., Lam, S.K., Wolf, B., Kiese, R., Butterbach-Bahl, K., Chen, D., Li, Z.,
570 Yan, X., 2020. Simultaneous quantification of N₂, NH₃ and N₂O emissions from a flooded paddy
571 field under different N fertilization regimes. *Glob. Chang. Biol.* 26, 2292-2303.

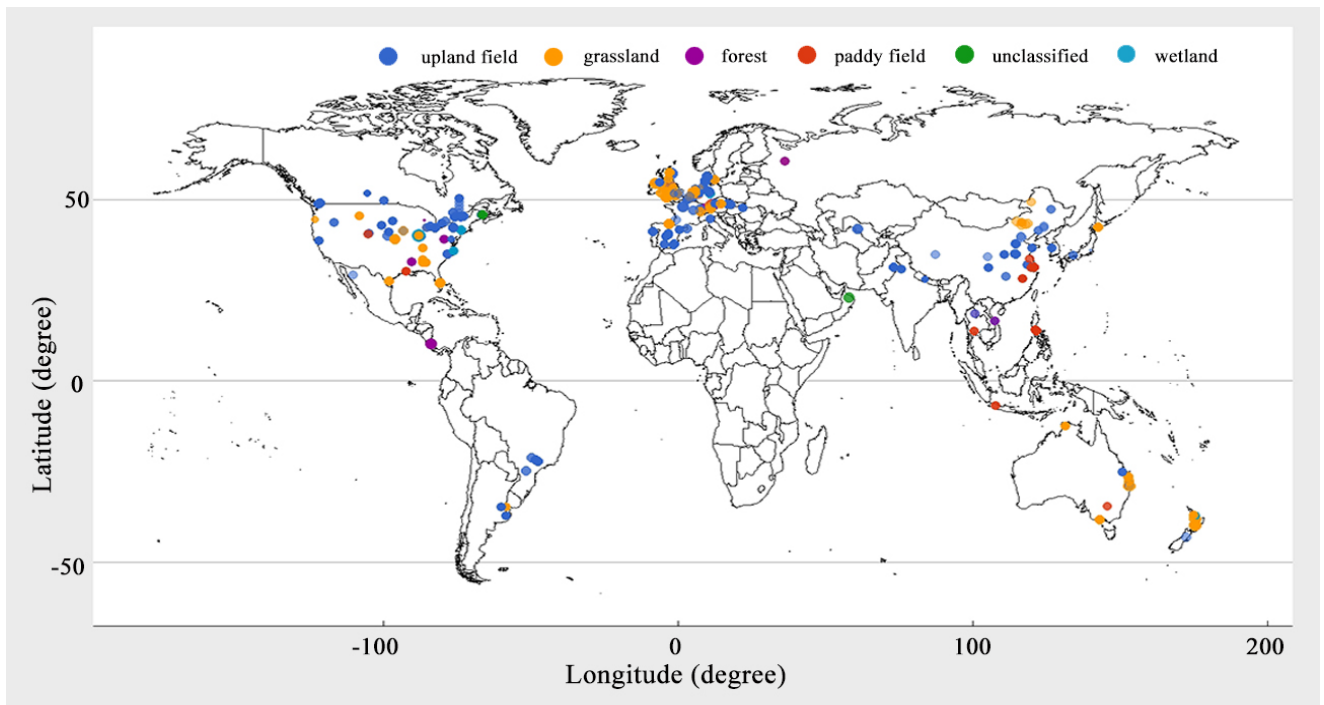
572 Zaman, M., Nguyen, M., Matheson, F., Blennerhassett, J., Quin, B., 2007. Can soil amendments
573 (zeolite or lime) shift the balance between nitrous oxide and dinitrogen emissions from pasture
574 and wetland soils receiving urine or urea-N? *Soil Res.* 45, 543-553.

575 Zaman, M., Nguyen, M.L., 2010. Effect of lime or zeolite on N₂O and N₂ emissions from a
576 pastoral soil treated with urine or nitrate-N fertilizer under field conditions. *Agric. Ecosyst.*
577 *Environ.* 136, 254-261.

578 Zaman, M., Nguyen, M.L., Simek, M., Nawaz, S., Khan, M.J., Babar, M.N., Zaman, S., 2012.
579 Emissions of nitrous oxide (N₂O) and di-nitrogen (N₂) from the agricultural landscapes, sources,
580 sinks, and factors affecting N₂O and N₂ ratios. In: Liu, G. (Ed.), *Greenhouse Gases - Emission,*
581 *Measurement and Management.* IntechOpen, pp. 3-32.

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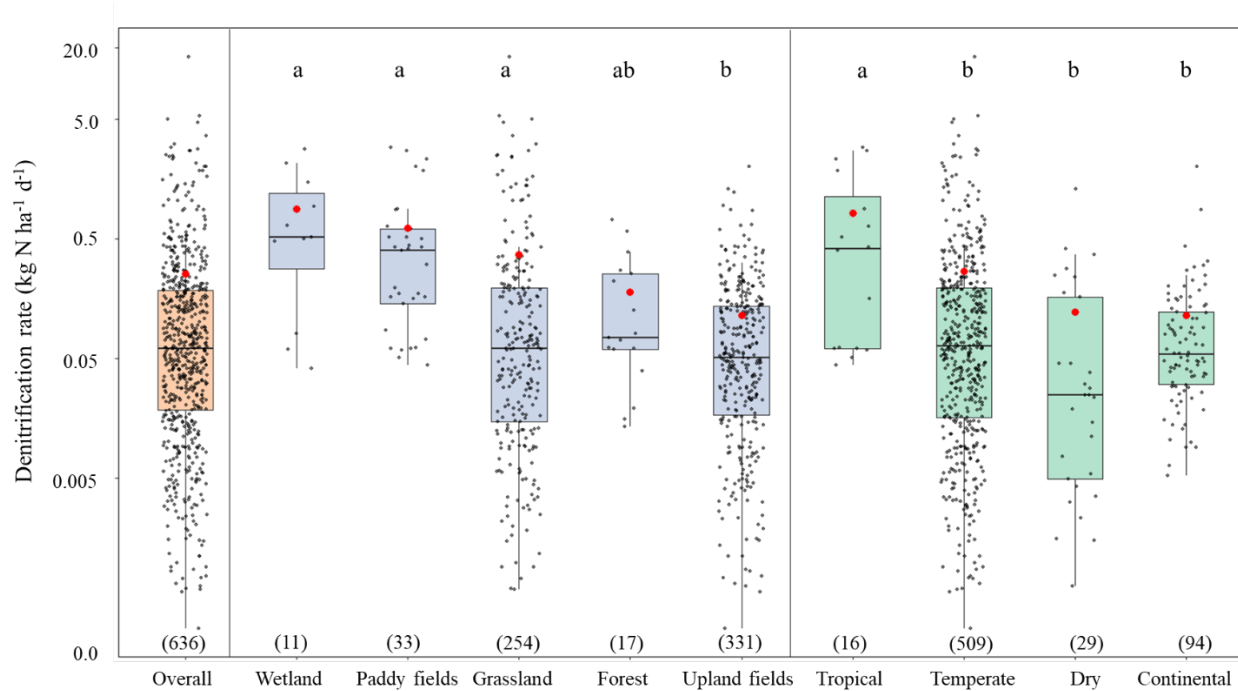
Figure 1. Location of study sites included in the database

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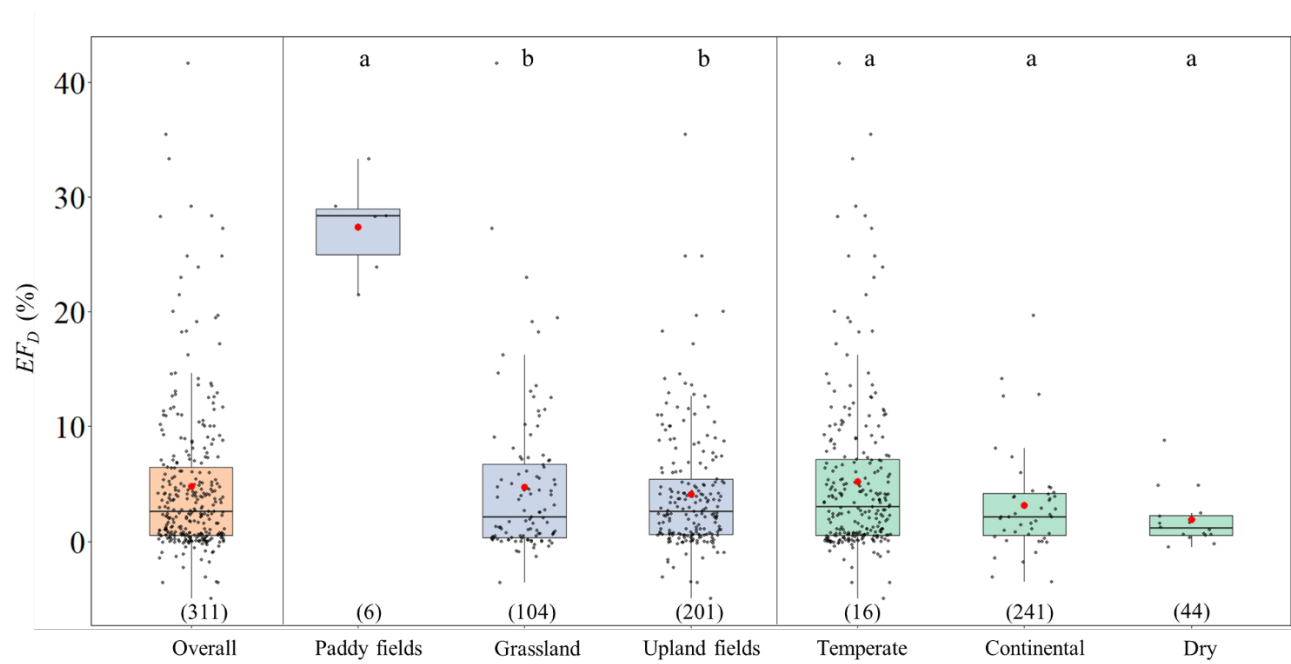


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591 Figure 2. Denitrification rate across land uses and climatic zones from field experiments. Values
 592 in parentheses represent the number of observations. Different letters on the top indicate that the
 593 mean values are significantly different at $p < 0.05$.

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597 Figure 3. EF_D across land uses and climatic zones from field experiments. Values in parentheses

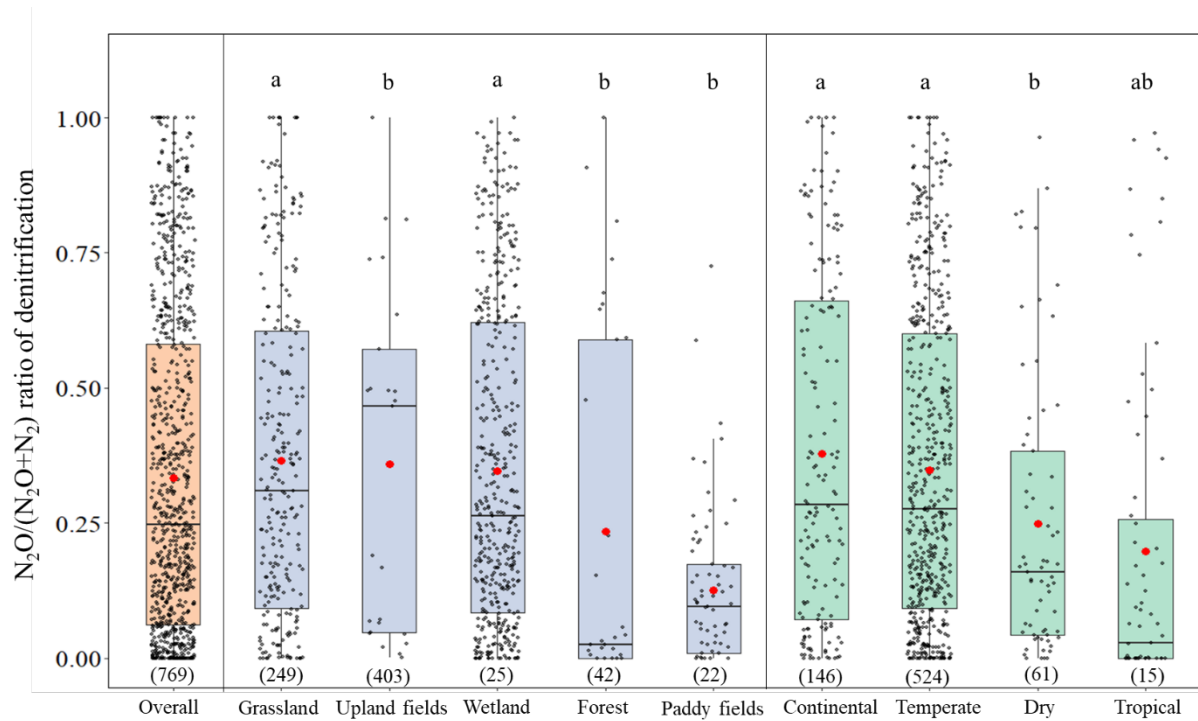
598 represent the number of observations. Different letters on the top indicate that the mean values

599 are significantly different at $p < 0.05$.

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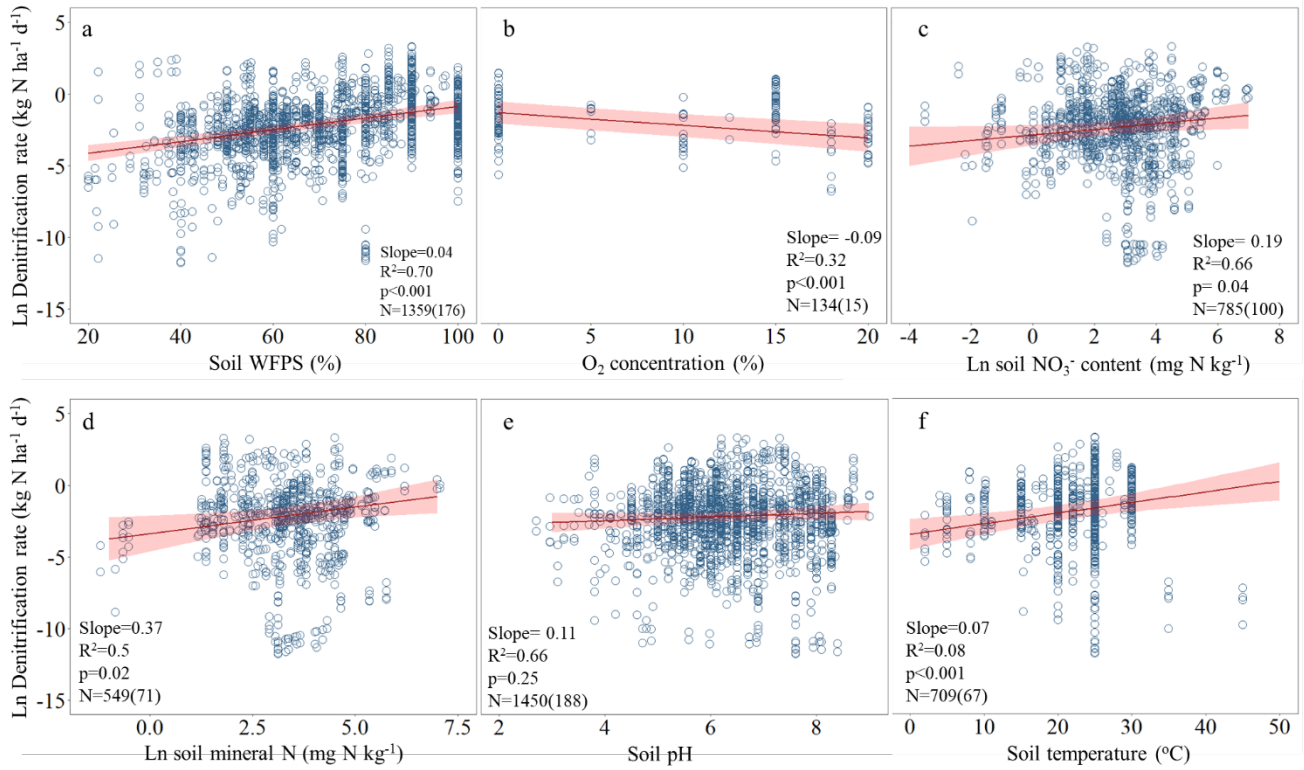


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604 Figure 4. The $N_2O/(N_2O+N_2)$ ratio of denitrification across climatic zones and land use types.

605 Values in parentheses represent the number of observations. Different letters on the top indicate

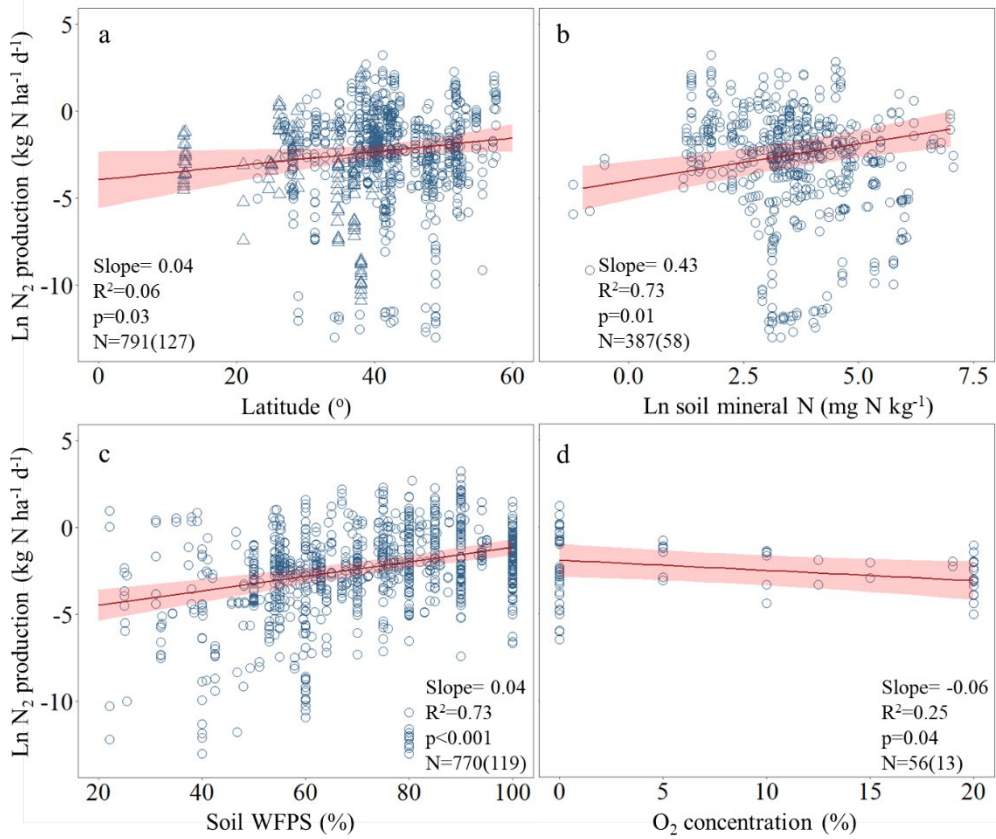
606 that the mean values are significantly different at $p < 0.05$.



607

608 Figure 5. Relationships between soil denitrification rate and a) soil WFPS, b) soil O₂ concentration,
 609 c) soil NO₃⁻ content, d) soil mineral N, e) soil pH and f) soil temperature. The red lines indicate
 610 the slopes from the linear mixed effects models and the red shadings represent the 95% confidence
 611 intervals. N in the figure represents the number of observations and the values in parentheses the
 612 number of studies.

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615 Figure 6. Relationships between soil N₂ emissions and a) latitude (circles: the Northern

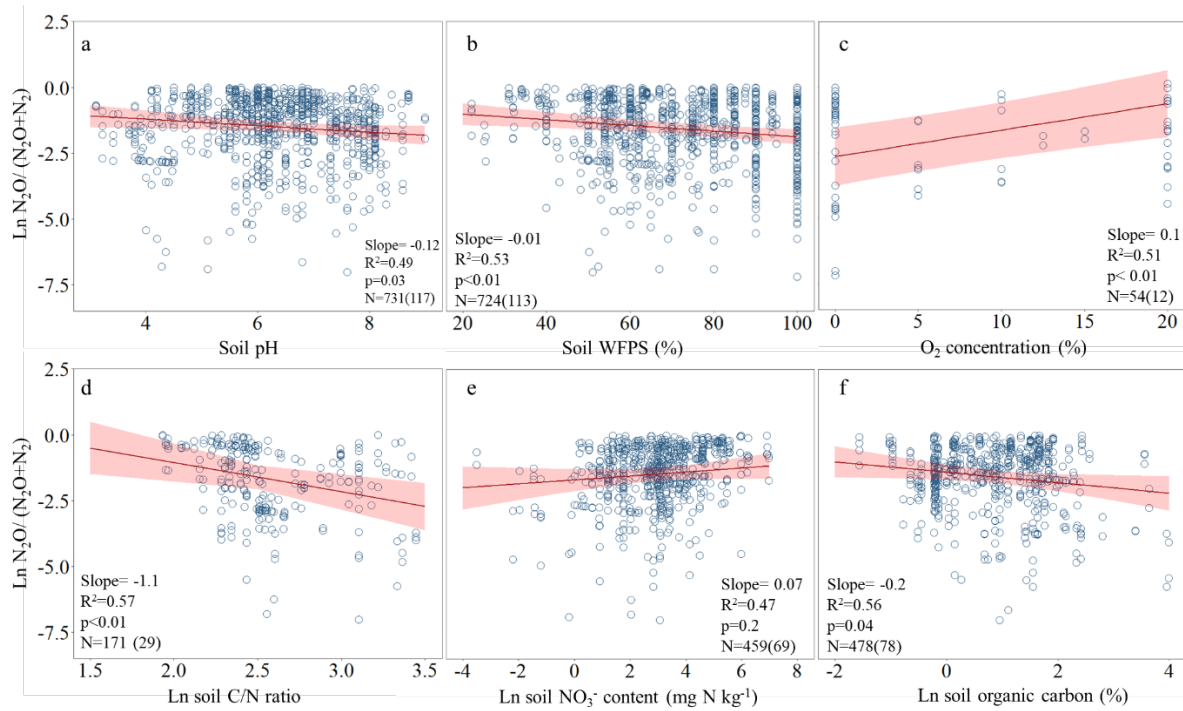
616 Hemisphere; triangles: Southern Hemisphere), b) soil mineral N, c) soil WFPS and d) soil O₂

617 concentration. The red lines indicate the slopes from the linear mixed effects models and the red

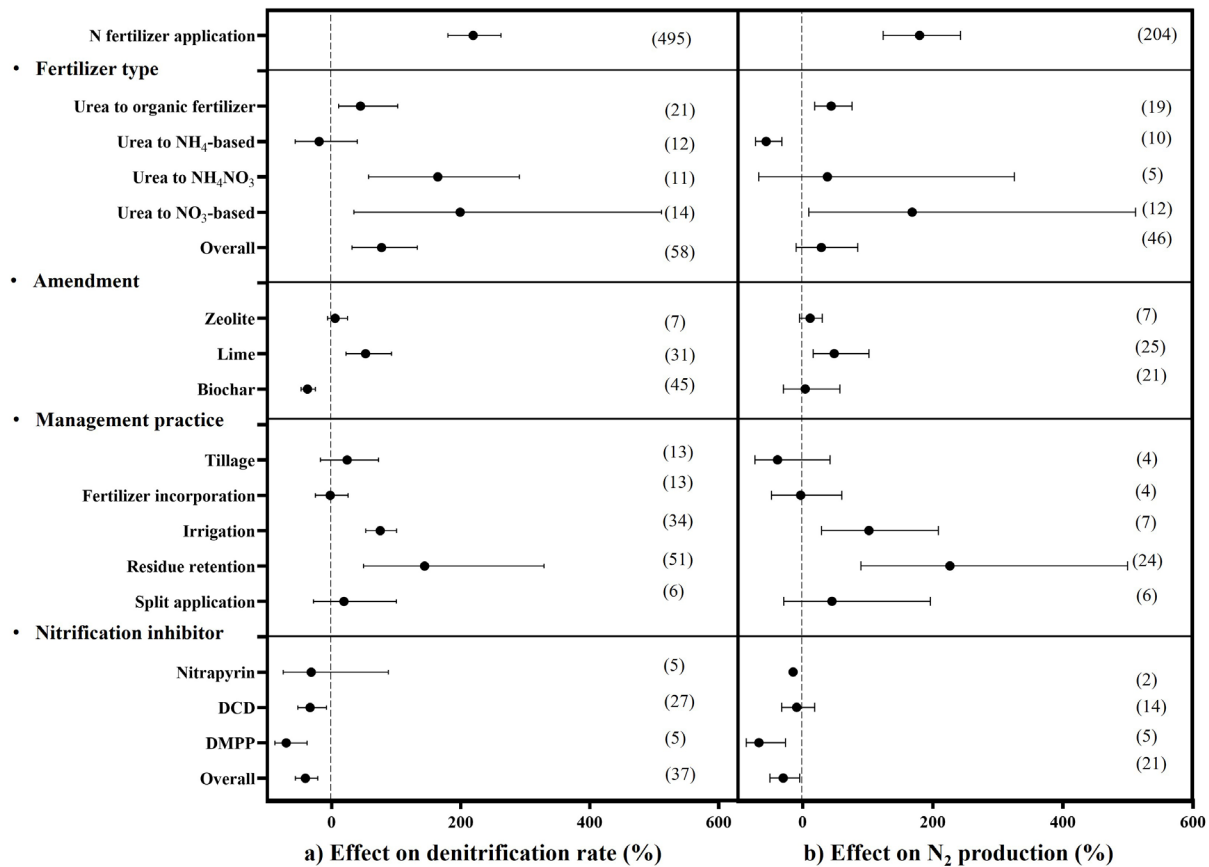
618 shadings represent the 95% confidence intervals. N in the figure represents the number of

619 observations and the values in parentheses the number of studies.

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 622 Figure 7. Relationships between soil $N_2O/(N_2O+N_2)$ ratio and a) soil pH, b) soil WFPS, c) soil O_2
 623 concentration, d) soil C/N ratio, e) soil NO_3^- content and f) soil organic C. The red lines indicate
 624 the slopes from the linear mixed effects models and the red shadings represent the 95% confidence
 625 intervals. N in the figure represents the number of observations and the values in parentheses the
 626 number of studies.



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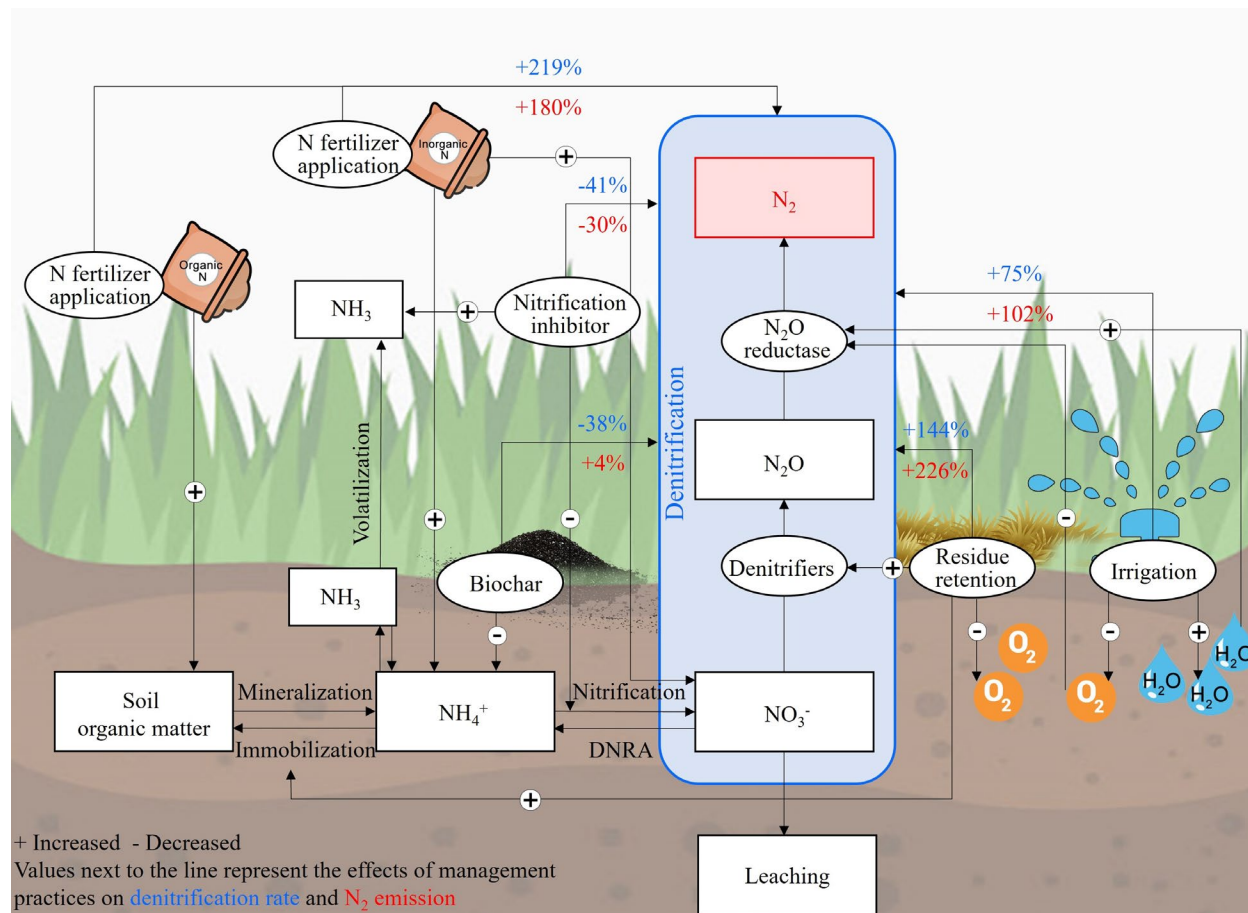
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Figure 8. Effect of N application, fertilizer type, amendment, management practice and nitrification inhibitor on a) denitrification rate and b) N₂ production. Means and 95% confidence intervals are depicted. Numbers of experimental observations are in parentheses. DCD: dicyandiamide, DMPP: 3,4-Dimethylpyrazole phosphate, Nitrapyrin: 2-chloro-6-(trichloromethyl) pyridine.



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 641 Figure 9. The effects of management practices on soil denitrification rate, N₂ emission and
 642 associated soil N transformations. Values presented were obtained from the meta-analysis in this
 643 study. '+' and '-' denote increased and decreased responses to management practices. DNRA:
 644 dissimilatory nitrate reduction to ammonium.