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Geomorphic control on the δ^{15} N of mountain forest

R. G. Hilton¹, A. Galy², A. J. West³, N. Hovius², and G. G. Roberts⁴

¹Department of Geography, Durham University, Durham, DH1 3LE, UK ²Department of Earth Sciences, University of Cambridge, Cambridge, CB2 3EQ, UK ³Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089, USA ⁴Bullard Laboratories, Department of Earth Sciences, University of Cambridge, Cambrid

⁴Bullard Laboratories, Department of Earth Sciences, University of Cambridge, Cambridge, CB3 0EZ, UK

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Correspondence to: R. G. Hilton (r.g.hilton@durham.ac.uk)

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Abstract

Mountain forests are subject to high rates of physical erosion which can export particulate nitrogen from ecosystems. However, the impact of geomorphic processes on nitrogen budgets remains poorly constrained. We have used the elemental and isotopic composition of soil and plant organic matter to investigate nitrogen cycling in the 5 mountain forest of Taiwan, from 24 sites with distinct geomorphic (topographic slope) and climatic (precipitation, temperature) characteristics. The organic carbon to nitrogen ratio of soil organic matter decreased with soil ¹⁴C age, providing constraint on average rates of nitrogen loss using a mass balance model. Model predictions suggest that present day estimates of nitrogen deposition exceed contemporary and historic 10 nitrogen losses. We found ~ 6 % variability in the stable isotopic composition (δ^{15} N) of soil and plants which was not related to soil ¹⁴C age or climatic conditions. Instead, δ^{15} N was significantly, negatively correlated with topographic slope. Using the mass balance model, we demonstrate that the correlation can be explained by an increase in nitrogen loss by non-fractioning pathways on steeper slopes, where physical erosion 15 effectively removes particulate nitrogen. Published data from forest on steep slopes are consistent with the correlation, demonstrating that variable physical erosion rates can significantly influence soil δ^{15} N, and that particulate nitrogen export is a major loss

term in the nitrogen budget of mountain forest.

20 **1** Introduction

Nitrogen (N) is essential to primary productivity in the terrestrial biosphere (Evans, 1989; Vitousek and Howarth, 1991). The stock of bioavailable N influences an ecosystem's ability to buffer increases in atmospheric carbon dioxide through enhanced productivity (Oren et al., 2001), and also determines the impact of anthropogenic N deposition on plant growth and soil biogeochemistry (Aber et al., 1989; Matson et al., 1999;

²⁵ sition on plant growth and soil biogeochemistry (Aber et al., 1989; Matson et al., 1999; Zaehle et al., 2011). For these reasons, there have been considerable efforts to better



understand the processes and rates of N loss from forests, and the factors which inhibit or amplify nutrient export (e.g. Hedin et al., 1995; Howarth et al., 1996; Lewis et al., 1999; Saunders et al., 2006; Schlesinger et al., 2006).

- The loss of N from ecosystems can result in lateral fluxes of N compounds across 5 the landscape. Rivers carry a signature of the dominant processes of N loss (gaseous, dissolved, particulate) and the rates at which they occur throughout catchments (e.g. Houlton et al., 2006; Brookshire et al., 2012a) and river loads from undisturbed tropical forests reveal that particulate nitrogen (PN) export can be a significant loss term (Lewis et al., 1995). For example, the Madeira and Solimões rivers which drain the Andes to the Amazon River (McClain and Naimen, 2008) export ~ 0.2 t N km⁻² yr⁻¹ and 10 ~ 0.4 t N km⁻² yr⁻¹ of PN, respectively. The PN flux is the largest single component of N exported from these catchments, and is approximately equal to the total dissolved N loss (Lewis et al., 1999). Even higher rates of PN export can occur from forests undergoing rapid physical erosion (Dadson et al., 2003; Milliman and Farnsworth, 2011), with mountain rivers exporting particulate organic carbon (POC) derived from plant and soil 15 organic matter at rates > $10 \text{ tCkm}^{-2} \text{ yr}^{-1}$ (Kao and Liu, 2000; Hilton et al., 2008, 2012; Townsend-Small et al., 2008; Hatten et al., 2012). Despite its potential importance, the
- impact of physical erosion and PN loss on N cycling in ecosystems remains poorly constrained (Brenner et al., 2001; Amundson et al., 2003; Quinton et al., 2010). This
 is particularly the case for mountain forests, where PN transfers are not typically considered alongside dissolved N export (Saunders et al., 2006; McGroddy et al., 2008; Brookshire et al., 2012a; Huang et al., 2012), evolution of soil carbon stocks or POC

transfer (Yoo et al., 2006; Hilton et al., 2008, 2012).

Here we examine N cycling in the subtropical mountain forest of the Central Range,
 Taiwan, and assess the role of physical erosion as a driver of N loss in ecosystems.
 Erosion rates in this mountain belt are 3–6 mm yr⁻¹ (Dadson et al., 2003), amongst the highest in the world (Milliman and Farnsworth, 2011). Topographic slope is the fundamental control on particulate export at the hillslope scale (Gilbert, 1909; Culling, 1960; Roering et al., 2001; Dietrich et al., 2003). Therefore, we have collected soil and plant



organic matter from sites which randomly sample slope angle as an environmental variable and measured its N isotopic composition (reported as δ¹⁵N‰), and organic carbon to nitrogen ratio (C/N), as well as the radiocarbon concentration of soil organic matter (reported as ¹⁴C age, yr). The sites also span climatic conditions (temperature, precipitation), which are thought to play an important role in N cycling in ecosystems (Amundson et al., 2003). These samples provide a record of the integration of N inputs and outputs from the mountain forest over decades to millennia (Fig. 1) (Delwiche and Steyn, 1970; Mariotti et al., 1980; Handley and Raven, 1992; Högberg and Johannisson, 1993; Martinelli et al., 1999; Robinson, 2001) and in combination with a mass
balance model (Brenner et al., 2001) our measurements give new insight into the pathways of N loss and N cycling in mountain forest.

2 Study area and site characteristics

Taiwan is located at 22–25° N on the West Pacific margin at the convergence zone between the Eurasian and Philippine Sea plates. The Central Range mountains form the topographic spine of the island, ~ 350 km long and ~ 50 km wide with numerous 15 peaks over 3000 m (Fig. S1). Mean annual precipitation (MAP) averages ~ 2500 mm and can reach 6000 mm (Dadson et al., 2003). Much of this falls as rain during tropical cyclones that impact the island between June and October. The tectonic and climatic regime combine to produce high rates of physical erosion (Dadson et al., 2003) and build catchments where steep slopes are prevalent (Hilton et al., 2012). Vegetation 20 grows up to the crests of the highest ridges and on the steep slopes, with the subtropical forest containing Ficus, Machilus, Castanopsis, Quercus, Pinus, Tsuga, and Picea (Su, 1984). The above ground standing biomass stock in mixed conifer-hardwood forest of Taiwan is ~ 22000 t km⁻² (West et al., 2011), similar to the average estimated for the tropics (Dixon et al., 1994), making the mountain forest of Taiwan a suitable 25 location to study the influence of climatic and geomorphic gradients on N cycling.



Samples were collected from sites on two east-west trending transects separated north-south by ~ 100 km (Fig. S1). The northern transect was ~ 30 km long and located mostly in the Liwu River catchment (435 km²). The southern leg was ~ 40 km long in the catchment of the Wulu River (639 km²). Rates of POC export from these and other mountain catchments in Taiwan have been determined previously from direct sampling of rivers, returning yields of POC from vegetation and soil (Kao and Liu, 2000; Hilton et al., 2008, 2012) after accounting for fossil POC input to the river sediments (Hilton et al., 2010). According to these estimates, the inter-annual rate of POC export from the Liwu and Wulu catchments was 6.8 ± 2.7 tC km⁻² yr⁻¹ and 13.8 ± 4.8 tC km⁻² yr⁻¹, respectively (Hilton et al., 2012). While some of this material may have derived from erosion of biomass by slope-clearing bedrock landslides (Hilton et al., 2011; West et al., 2011), soil loss via overland flow is important for POC export from mountainous terrain (Larsen et al., 1999; Hilton et al., 2008, 2012; Walker and Shiels, 2008; Hatten et al.,

2012). Soil organic matter in Taiwan has an organic carbon to nitrogen ratio \sim 12 (Kao

and Liu, 2000). Hence, measured rates of POC export could correspond to a PN export

of $\sim 1 \text{ t N km}^{-2} \text{ yr}^{-1}$ from the mountain forest. This estimate is consistent with other

measurements from Taiwan in the Lanyang River catchment (820 km²; Fig. S1), located

in the north east where erosion rates are lower (Dadson et al., 2003), where PN export

From 24 sites we collected 13 soil samples and 23 plant samples (Table S1). Sam-

ples were collected at discrete elevations (m), recorded using handheld GPS, to vary mean annual temperate (MAT). MAT was estimated using the sample site elevation and

a saturated adiabatic lapse rate of 5°C km⁻¹ combined with measured MAT (1981– 2010) at sea level of 23.4°C and 24.5°C at Hualien (23.98°N, 121.60°E, northern

transect) and Taitung (22.76° N, 121.15° E, southern transect), respectively (Fig. S1).

The predicted MAT at Yushan (3950 m, 23.47° N, 120.26° E), 4.2°C, is within 1°C of

the measured value (climate statistics for Taiwan, Central Weather Bureau, Taiwan

http://www.cwb.gov.tw/eng/index.htm). To check that the isotopic composition of organic matter was representative of the sites, duplicate soil samples were collected

from vegetation and soil is 0.4 ± 0.2 t N km⁻² yr⁻¹ (Kao and Liu, 2000).

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at two sites, two plant species were sampled at four sites and six paired samples of soil and plant organic matter were collected.

In line with the objectives of this study, other attributes were not considered in site selection and are assumed to be sampled randomly. Decadal averaged MAP (mm) was obtained from a digital map gridded at 1 × 1 km (Dadson et al., 2003). Hillslope 5 angle (θ , °) was determined using ArcInfoTM software, from a digital elevation model $(40 \times 40 \text{ m grid})$ and sampled over a 100 m length scale which is appropriate when considering erosion laws in mountain landscapes (Dietrich et al., 2003). Topographic slope was recorded as $\sin\theta$. The sample sites ranged between 530 m and 3190 m elevation, 7 °C to 21.9 °C MAT, 2060 mm to 3500 mm MAP, and had a slope angle θ between 7° and 50° (0.12 to 0.76 slope) (Table S1). We note that significant correlations exist between attributes of our soil sites (Table 1), with a negative relationship between MAT and MAP (P = 0.03) reflecting orographic forcing of precipitation, and a positive relationship between MAT and slope angle (P = 0.02). The latter is not observed for plant sample sites (Table 2) and there is no physical reason why these two variables 15 should be correlated.

3 Materials and methods

3.1 Samples

Plant samples were collected in March 2006 from *Pinus morrisonicola* (Taiwan white pine), selected for its ubiquitous presence across the full elevation range of forest (Su, 1984). Stems ~ 5–10 mm in diameter (to provide an integration of several growing seasons) and less than ~ 30 cm long were cut from live adult (> 4 m) specimens. In addition, stems of ~ 1 m tall *Cymbopogon* sp. grasses were collected to investigate interspecies heterogeneity. Stems were stored in sterile sample bags and frozen less
than one week after collection. After storage for one month, plant samples were oven



dried at < 80 °C to remove remaining moisture. Bark was removed from pine stems and samples cut into \sim 1 mg pieces and stored in sealed glass vials.

Soil samples correspond to A–E soil horizons (variable humified organic matter intimately mixed with coarse and fine mineral fractions, bearing little structure of the

original bedrock) were obtained at the same time as plants. Approximately 500 cm³ of bulk material were collected over a depth of ~ 10 cm and sealed in sterile bags, dried at 80 °C within one week of collection and decanted for dark storage within sealed sterile bags. To obtain an integrated bulk soil sample at each site the entire sampled mass was then homogenised using a Cyclostec mill grinder. Inorganic carbon was removed
 from soils using a HCl leach (Hilton et al., 2010).

3.2 Measurement procedures and data analysis

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Weight percent organic C (C_{org} , %) and N were determined on plant material and soil (following inorganic carbon removal) by combustion at 1020 °C in O₂ within a Costech elemental analyser (EA), normalised to an average of acetanilide standards and corrected for internal and procedural blanks as reported elsewhere (Hilton et al., 2010). Stable isotopes of organic C and N were analysed by a MAT-253 isotope ratio mass

- spectrometer coupled to the EA via Conflo-III and normalised based on measured values of standards (IAEA: N-1, NO₃) and laboratory standards (oxalic acid and porano), corrected for internal and procedural blanks and reported in δ^{15} N and δ^{13} C notation relative to air (Mariotti, 1983) and Vienna Peedee Belemnite, respectively. For plant
- ²⁰ relative to air (Mariotti, 1983) and Vienna Peedee Belemnite, respectively. For plant samples, to obtain desired amounts of N₂ for isotopic analysis large amounts of CO₂ were produced. A CARBOSORBTM trap was used to scrub CO₂ prior to its introduction to the EA GC-column. For soils, ¹⁴C concentrations were determined, after graphitisation of CO₂, by accelerator mass spectrometry at the UK National Environmental Research Council Radiocarbon Facility and are reported as ¹⁴C age.
 - Precision (2 σ) and accuracy of stable isotope measurements were determined using IAEA 600 and USGS-40 standards. Measured mean δ^{15} N were 1.2±0.2‰ (IAEA 600,



 $\pm 2\sigma$, n = 28) and $-4.5 \pm 0.5\%$ (IAEA USGS-40, $\pm 2\sigma$, n = 18) and mean $\delta^{13}C -27.6 \pm 0.3\%$ (IAEA 600, $\pm 2\sigma$, n = 30), indicating average accuracies of 0.1% and -0.1% for $\delta^{15}N$ and $\delta^{13}C$, respectively. Further replicates of soil samples returned average 2σ of $\pm 0.4\%$ (n = 8) and $\pm 0.3\%$ (n = 19), for $\delta^{15}N$ and $\delta^{13}C$, respectively. Average precision on ¹⁴C age measurements was 72 yr (2σ). The inorganic removal procedure did not alter the measured $\delta^{15}N$ of the soil materials beyond this precision according to a comparison with aliquots not subjected to the acid leach, which conforms with results from soil materials elsewhere (Brodie et al., 2011), nor did it alter the ¹⁴C age and $\delta^{13}C$ of treated IAEA standards (Hilton et al., 2008). The measured variables were analysed for statistically significant inter-correlation using OriginProTM. Mean values of sample sets are reported \pm the standard error of the mean throughout.

4 Results

4.1 Vegetation

Stems of *P. morrisonicola* had an average $\delta^{15}N=-0.4\pm0.7\%$ (n = 14) and exhibited a ~ 6% range from -2.4% to 3.7% (Fig. 2; Table S2). The grass samples collected at the same site (n = 4) had a small (1.0%), non-systematic average difference in $\delta^{15}N$ from *P. morrisonicola*, suggesting that inter-species variability in $\delta^{15}N$ was minor when compared to range of measured values. For *P. morrisonicola*, $\delta^{15}N$ was significantly (P = 0.006) negatively correlated with slope (Fig. 3), with no statistical link between $\delta^{15}N$ and MAP or MAT. When the two species were combined (n = 23) the mean $\delta^{15}N=-0.9\pm0.5\%$ and the negative correlation between $\delta^{15}N$ and slope angle was strengthened (P = 0.003), remaining the only statistical link to a site attribute (Table 2). *P. morrisonicola* stems had an average $\delta^{13}C=-28.1\pm0.3\%$ (n = 14) and $\delta^{13}C$ values were positively correlated with elevation (P = 0.003) in agreement with trends observed in C3 plants elsewhere (Körner et al., 1988). This suggests that the sampled organic matter was in equilibrium with environmental conditions at the sites.



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Cymbopogon sp. had higher δ^{13} C values (Table S2), indicative of a C4 plant (Smith and Epstein, 1971).

4.2 Soil

The bulk C/N of soil organic matter ranged between 3 and 14 (Table S3) and were
 similar to those reported elsewhere in Taiwan (Kao and Liu, 2000). A significant negative correlation (*P* = 0.0004) existed between C/N and ¹⁴C age of bulk soil across all sample sites (Table 1). This correlation is not compatible with mixing of fossil organic matter from sedimentary bedrock (no ¹⁴C, C/N ~ 5–10) with vegetation (Hilton et al., 2010). Instead, the ¹⁴C depletion represents aging of organic matter. Soil ¹⁴C age was not correlated with the climatic and geomorphic characteristics of the sample sites, or with δ¹⁵N values (Table 1).

The average δ^{15} N of bulk soil was $4.0 \pm 0.5\%$ (n = 13) and ranged over ~ 6% from 0.7% to 6.5% (Fig. 2). These values are similar to published measurements from soils in other locations in Taiwan (Kao and Liu, 2000; Liu et al., 2006). δ^{15} N values of duplicate and triplicate samples collected at two of the sites (Tables S1 and S3) were indistinguishable within the analytical uncertainty of 0.4%, with means of 6.2 ± 0.3% (n = 2) and 4.5±0.3 (n = 3), indicating that measured soil δ^{15} N values can be taken as representative site averages.

Soil δ^{15} N values were significantly, negatively correlated with slope (P = 0.025; Ta-²⁰ ble 1) and displayed a similar relationship as plant δ^{15} N (Fig. 3). A negative relationship existed between δ^{15} N and MAT (P = 0.008) and δ^{15} N was positively correlated with MAP, but not significantly at the 95 % level (P = 0.07). Correlations amongst δ^{15} N and MAT and MAP were not observed in the larger, vegetation sample set (Table 2). The statistical link between these variables in the soil data set may be the product of the negative correlation between MAT and slope at the soil sites (Table 1). It can explain why the soil δ^{15} N-MAP and δ^{15} N-MAT trends are opposite to those generally observed elsewhere in tropical forest (Amundson et al., 2003). Measured soil δ^{15} N values were higher than plants (Fig. 2) and mean values of these populations were significantly different at the 0.05 level (one-way ANOVA; P < 0.0001). The offset between soil and plant organic matter, $\Delta \delta^{15}$ N_{s-p}, was consistent with an uptake of ¹⁵N-depleted N by plants (Delwiche and Steyn, 1970; Handley and Raven, 1992) with the average $\Delta \delta^{15}$ N_{s-p} = 4.1 ± 0.3% (n = 6; Table S2) relatively constant across the range of sampled climatic and geomorphic conditions (MAT 10 °C to 20 °C, MAP 2480 mm and 3200 mm, slope angle 20° to 50°). $\Delta \delta^{15}$ N_{s-p} was similar to global-scale predictions from ambient MAP and MAT (Amundson et al., 2003) and also consistent with the 4±2% offset between the intercepts of the linear trends between slope and δ^{15} N for soil and plants (Fig. 3). The identical gradients of these trends in the independent datasets further supports the statistical analysis which revealed slope as the primary site attribute linked to δ^{15} N.

5 Discussion

5.1 Constraints on rates of N flux from the ecosystem

- The balance between the input of N to an ecosystem and the rate of N loss from soil places a first order control on the amount of bioavailable N for productivity (Fig. 1). Constraining the fluxes of N and the operation of this mass balance is important for understanding how an ecosystem may response to ongoing anthropogenic perturbation of the N cycle (Matson et al., 1999; Zaehle et al., 2011). In our samples, the soil C/N decreases with increasing ¹⁴C age over centuries to millennia (Table 1). This suggests retention of N relative to C in soils across this mountain forest, consistent with heterotrophic consumption of organic compounds. However, it does not preclude N loss from the soil, and here we seek to model the observed C/N evolution to provide insight to the rates of N loss to the environment.
- ²⁵ A multi-component, multi-pool soil model (Trumbore, 1993; Baisden et al., 2002a,b; Manzoni and Porporato, 2009) is not appropriate here, because the soil C/N and ¹⁴C



measurements were made on homogenised, bulk surface soil, integrating a range of grain sizes and organic-mineral aggregates. In addition, soils in the forested mountains of Taiwan are thin, with the base of the saprolite typically at < 0.8 m below surface (Tsai et al., 2001). As such, transport of organic material to deeper horizons can be considered negligible (cf. Yoo et al., 2006). Therefore, we use a single pool soil model, which describes the evolution of bulk soil N as a mass balance of net inputs and outputs (Fig. 1; Brenner et al., 2001). The soil N content over a constant depth (N_s, t N km⁻²) evolves at a rate (t N km⁻² yr⁻¹):

$$\frac{\mathrm{dN}_{\mathrm{s}}}{\mathrm{d}t} = I_{\mathrm{ex}} - k_{\mathrm{ex}} \cdot \mathrm{N}_{\mathrm{s}} \tag{1}$$

¹⁰ where I_{ex} (tN km⁻² yr⁻¹) is the sum of external N inputs to the ecosystem (wet and dry N deposition) and k_{ex} is the rate constant of the ensemble of pathways of N loss (inorganic and organic, gaseous, dissolved and particulate) to the environment (yr⁻¹). Here we do not attempt to deconvolve these k_{ex} pathways using C/N alone, instead we use δ^{15} N to examine them in more detail in Sect. 5.2. The model assumes that internal N cycling between soil and vegetation (Fig. 1) operates at a steady state. When considering periods shorter than the time required for soil N to turnover, ~ 50–100 yr (Brenner et al., 2001), this assumption does not hold and the model should be adapted to include internal N cycling (e.g. Menge et al., 2009; Brookshire et al., 2012b) which can show marked inter-annual variability (e.g. Owen et al., 2003). However, for periods longer than this turnover time, the evolution of N_s is principally governed by the external loss rate k_{ex} (Brenner et al., 2001; Menge et al., 2009), and Eq. (1) is adequate.

By analogy, the rate of change in soil organic C content (C_s , t C km⁻²) through time can also be described by mass balance. Here the soil input is by supply of plant-fixed carbon:

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$$\frac{dC_s}{dt} = j_s \cdot C_p - j_{ex} \cdot C_s$$

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(2)

where j_s (yr⁻¹) is the rate constant of organic C supply from plants with a C content C_p (t C km⁻²) and j_{ex} (yr⁻¹) is the rate constant of C loss from soils, adapted from Baisden et al. (2002a). Again, we consider centennial to millennial timescales (> soil C turnover time) for which a steady state assumption is relevant, where $C_p \approx C_s$ (Dixon et al., 1994). The mass balance can then be simplified to:

$$\frac{\mathrm{d}\mathbf{C}_{\mathrm{s}}}{\mathrm{d}t} = -j_{\mathrm{net}} \cdot \mathbf{C}_{\mathrm{s}}$$

5

where the variable j_{net} (yr⁻¹) is the net C loss rate constant.

N_s and C_s are modelled at 50 yr intervals to examine the average rate of N loss from soil integrated over the full dataset. This approach is comparable to considering N export at the catchment-scale, where rivers integrate over large areas > 100 km² (Lewis et al., 1999). The starting condition is set by the three "modern" soils (assigned ¹⁴C age = 5±36 yr) with an average C/N = 12 (Table S3). Changes in ¹⁴C abundance are attributed fully to radioactive decay of the bulk soil C pool through time, with a decay constant of $1.2097 \times 10^{-4} \text{ yr}^{-1}$ (Godwin, 1962) and the 50 yr resolution of the model means that bomb-¹⁴C input is not considered (Levin and Hesshaimer, 2000). The variables I_{ex} , k_{net} and j_{net} are then used to minimise the misfit between modelled and measured soil C/N with age (Fig. 4). Best fit solutions have co-variation of j_{net} and k_{ex} for a given I_{ex} . For $I_{ex} = 0 \text{ t N km}^{-2} \text{ yr}^{-1}$, the minimised misfit solutions of the model yield a linear relationship, $k_{ex} = 1.017 \times j_{net} - 0.00033$, with a relative C/N misfit of 19.9%. For $I_{ex} > 0 \text{ t N km}^{-2} \text{ yr}^{-1}$, model solutions exhibit a positive non-linear relationship between j_{net} and k_{ex} .

To explore the range of k_{ex} values permitted by the model best fit to the data, constraints on I_{ex} and j_{net} are required. A global compilation of data from tropical forests shows that I_{ex} values are commonly 0.2–0.4 t N km⁻² yr⁻¹ away from anthropogenic in-²⁵ puts (Brenner et al., 2001). For j_{net} , we note that our bulk soil samples show a net organic C loss with time. Young soils (¹⁴C age < 100 yr) have an average C_{org} of **Discussion** Paper BGD 9, 12593-12626, 2012 **Geomorphic control** on the $\delta^{15}N$ of mountain forest **Discussion** Paper R. G. Hilton et al. **Title Page** Introduction Abstract Conclusions References **Discussion Paper Tables Figures** Back Close **Discussion** Paper Full Screen / Esc **Printer-friendly Version** Interactive Discussion

(3)

3.11 ± 1.16 % (*n* = 4), which is significantly higher than older soils (¹⁴C age > 1000 yr), with an average $C_{org} = 0.67 \pm 0.07$ % (*n* = 5) and a minimum $C_{org} = 0.41$ % at 4169 yr (Table S3). This strongly suggests that $j_{net} > 0 \text{ yr}^{-1}$. In fact, assuming that C loss alone is responsible for the observed decrease in C_{org} with age, $j_{net} = 4.8 \times 10^{-5} \text{ yr}^{-1}$. This ⁵ is an upper bound, since it is likely that mineral dilution due to progressive weathering of underlying bedrock also acts to reduce C_s . When $I_{ex} = 0.3 \text{ tN km}^{-2} \text{ yr}^{-1}$ and $j_{net} = 4.8 \times 10^{-5} \text{ yr}^{-1}$, the fit to the data is strong ($r^2 = 0.63$; P = 0.0006), predicting $k_{ex} = 1.1 \times 10^{-3} \text{ yr}^{-1}$ (Fig. 4). The dependence of k_{ex} on I_{ex} can be explored using the quoted range from tropical forests, returning best fit solutions of $k_{ex} = 0.8 \times 10^{-3} \text{ yr}^{-1}$.

The model predictions for the average rate of N loss to the environment, k_{ex} , are consistent with the range of N loss constants in forest ecosystems worldwide (Brenner et al., 2001). However, it is worth remembering that our estimate of k_{ex} is an average for the whole dataset, derived from soils spread over >100 km (Fig. S1). Deviation from

- the best fit model (Fig. 4) may reflect local variability in N loss rate around this mean, which is to be expected, but it could also derive from the assumptions applied in the modelling. First, the model misfit was minimised to the measured soil C/N (y-axis), which is justified if the measured ¹⁴C ages (x-axis) result only from aging. However, physical erosion can result in thin soils which contain ¹⁴C dead, fossil organic C derived
- from sedimentary bedrock (Keller and Bacon, 1998). In Taiwan, bedrocks have C_{org} ~ 0.3 % which is incompletely oxidized in the environment (Hilton et al., 2010). Addition of fossil organic C could increase the ¹⁴C age of soil samples, affecting the oldest ¹⁴C ages with C_{org} values close to bedrock (Table S3). While mixing of fossil organic C (C/N~ 5–10, no ¹⁴C) with recent biomass is not consistent with the overall trend in the data (Fig. 4), its input could decrease the gradient between C/N and age. This would also occur if any pre-aged POC existed within the soil. Both these scenarios are not
- considered by the single pool model, but they can lead to an underestimation of the rate of change of C/N with time, lowering k_{ex} . Second, the assumption of a steady

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state exchange between plants and soil (Eq. 1 and 3) is probably not appropriate for young soils (< 100 yr, n = 4), which are prone to progressive N accumulation early in succession (Brenner et al., 2001; Walker and Shiels, 2008). By not accounting for this additional supply, k_{ex} is underestimated by the model at these young sites, but this assumption should not affect the soil C/N versus age relation on longer, multi-centennial time scales (Fig. 4).

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Mindful of these caveats, k_{ex} can be converted to an absolute N loss from soils and compared to measured rates of N loss. The C stock of soil litter in mixed conifer forest in Taiwan has been measured as $7 \pm 2 \times 10^3 \text{ tC km}^{-2}$ (Chang et al., 2006) and for the measured C/N of modern soil organic matter (C/N = 12), the corresponding soil N stock would be $570 \pm 160 \text{ tN km}^{-2}$. For this stock, the modelled best fit k_{ex} values (0.8– $1.5 \times 10^{-3} \text{ yr}^{-1}$) are equivalent to an initial N loss rate of $0.5-0.9 \text{ tN km yr}^{-1}$ (Fig. 4). This is within the lower range of contemporary estimates of N exports at the river catchment scale, which put leaching of dissolved inorganic N at $0.66 \pm 0.12 \text{ tN km}^{-2} \text{ yr}^{-1}$ (Kao 15 et al., 2004) and PN export up to ~ 1 t N km^{-2} \text{ yr}^{-1} (Sect. 2).

At present, estimated N losses from Taiwanese forest are exceeded by the estimated N deposition of ~ 1.8 t N km⁻² yr⁻¹ from local sources and emissions from continental Asia (Kao et al., 2004). If we consider additional N inputs though biological fixation (Vitousek and Howarth, 1991), a contemporary net input of at $\geq 0.2 t N \text{ km}^{-2} \text{ yr}^{-1}$ is supplied to the soil. In contrast, the modelled fit to the ¹⁴C and C/N trend suggests that

- ²⁰ supplied to the soil. In contrast, the modelled fit to the ¹⁴C and C/N trend suggests that the mountain forest of Taiwan operated with a much closer balance between inputs and outputs prior to the anthropogenic increase in N input (Fig. 4). This finding is consistent with observations from tropical forests elsewhere (Matson et al., 1999) and indicates that N saturation could increasingly affect the Taiwan mountain forest ecosystem if
- anthropogenic N deposition persists (Aber et al., 1989). Denitrification of a fraction of this accumulated N may produce regionally significant emissions of the greenhouse gas N₂O (e.g. Houlton et al., 2006) and is a poorly understood flux which warrants further assessment in Taiwan (Kao et al., 2004).



5.2 Insight to pathways of N loss from δ^{15} N

The evolution of the soil C/N with ¹⁴C age has been used to examine the average rate of N loss permitted by all of the soil data (Fig. 4). While this provides valuable first order constraint, individual sites are likely to have N loss rates which vary from this average, experiencing different pathways of N loss (e.g. dissolved, gaseous, particulate) 5 depending upon the ambient climatic and geomorphic conditions. While it is difficult to resolve this variability with C/N, the stable isotope values (δ^{15} N) of soils and plants can provide crucial insight. The δ^{15} N records an integration of N inputs and outputs and their isotopic signatures (Fig. 1) and δ^{15} N values are sensitive to the modes of N loss and the rates at which they occur (Mariotti et al., 1980; Högberg and Johannisson, 10 1993: Brenner et al., 2001: Robinson, 2001: Houlton et al., 2006), Hence we use δ^{15} N values from Taiwan to further interrogate the N cycle operating in this mountain forest. The decrease in C/N of soil organic matter with soil age is not accompanied by an increase in δ^{15} N values (Table 1). Therefore, the ~ 6 ‰ range in δ^{15} N recorded in both soil and plant organic matter is not simply the isotopic expression of accumulated min-15 eral N losses with aging of the soil (cf. Martinelli et al., 1999; Brenner et al., 2001). Instead, the variability in δ^{15} N, which is statistically correlated with slope (Tables 1 and 2), must reflect some combination of: (i) variable rates or δ^{15} N of external inputs (Kendall, 1998); and/or (ii) variable rates of fractionating and non-fractioning pathways of N loss (Fig. 1). With regard to N input, while spatial patterns of N deposition can 20 be complicated in mountainous terrain (Weathers et al., 2006), it is difficult to identify a process by which either the rate of N deposition or its isotopic composition depends systematically on slope. In addition, we are not aware of any study in which N fixation is linked to hillslope angle (Vitousek et al., 2002). Therefore, in analogy to other studies (e.g. Högberg and Johannisson, 1993; Martinelli et al., 1999; Robinson, 2001; Houlton 25 et al., 2006) we seek to explain the variability in δ^{15} N values by gradients in the processes that remove N (ii) and to provide a mechanistic explanation for the observed trend of δ^{15} N with slope (Fig. 3).



Hillslope angle is a principal control on the rate of physical erosion (Gilbert, 1909; Culling, 1960; Roering et al., 2001; Dietrich et al., 2003). The stability of hillslope materials is determined by the balance of the down-slope component of its weight and the frictional resistance to motion aided by the slope-normal component of the weight. As

the angle increases, this balance shifts in favour of the force driving motion. Therefore, the rate of soil erosion increases with slope $(\sin \theta)$ (Dietrich et al., 2003; Yoo et al., 2006) for both overland flow and mass wasting processes such as landsliding, and the local topographic gradient should rule the export of PN by soil erosion.

Assuming that erosion does not preferentially remove N from either soil or plant organic matter, PN loss should impart no direct isotopic fractionation on an ecosystem. However, it can change the bulk isotopic fractionation that the ecosystem experiences due to N loss, and indirectly control soil and plant δ^{15} N values (Brenner et al., 2001). To assess whether PN loss can explain the variability in δ^{15} N with slope (Fig. 3), the mass balance model (Eq. 1) can be used to examine δ^{15} N for a given range of k_{ex} values. The solutions at steady state can provide constraint on the sign of the δ^{15} N change and the maximum expected shifts (Brenner et al., 2001). In this case, the 15 N/¹⁴N ratio of the

ecosystem (R_s) is modified from the isotopic ratio of inputs (R_{ex}) by a bulk fractionation factor (α_{ex}) induced by k_{ex} :

$$R_{\rm s} = \frac{R_{\rm ex}}{\alpha_{\rm ex}}$$

²⁰ The rate constant $k_{\rm ex}$ (Eq. 1) includes processes that fractionate isotopes and others that do not (Fig. 1). Fractionating losses can be accounted for by the rate constant $k_{\rm f}$ (yr⁻¹). These include gaseous loss by denitrification and hydrological leaching of nitrified products, which are generally considered to leave the residual ¹⁵N-enriched by a fractionation factor $\alpha_{\rm f} < 1$ (Handley and Raven, 1992). Non-fractioning loss is con-²⁵ sidered here as PN export ($k_{\rm E}$, yr⁻¹) with $\alpha_{\rm E} = 1$. By definition, then, $k_{\rm ex} = k_{\rm f} + k_{\rm E}$ (Fig. 1) and so $\alpha_{\rm ex}$ can be determined from the relative contribution of fractionating



(4)

and non-fractioning losses to the total N loss:

$$\alpha_{\text{ex}} = \alpha_{\text{f}} \cdot \frac{k_{\text{f}}}{k_{\text{ex}}} + \alpha_{\text{E}} \cdot \frac{k_{\text{E}}}{k_{\text{ex}}}$$

Hence, R_s (Eq. 4) can vary due to changes in the nature of fractionating losses (α_f), or in the relative importance of non-fractioning pathways to the total N loss (k_F/k_{ex}).

Steady state values for R_s can be calculated using $R_{ex} = 0.0036765$ (atmosphere) 5 and $k_{ex} = 1 \times 10^{-3} \text{ yr}^{-1}$ derived from the best fit modelled solution of the C/N decrease with ¹⁴C age (Fig. 4). The observed range in ecosystem $\delta^{15}N$ (~ 6‰) is returned for α_{ex} in the range 0.994 to 1.000 (Fig. 5). This can be achieved by varying k_{F} between 0 yr^{-1} and $1 \times 10^{-3} \text{ yr}^{-1}$ while keeping k_{ex} constant and $\alpha_{\text{f}} = 0.994$ (Eq. 5). For these settings and for a soil N stock of $\sim 570 \pm 160 \, t \, N \, km^{-2}$, the PN loss is found to range from 10 zero to 0.6 ± 0.2 t N km⁻² yr⁻¹ across the landscape and averaged over the residence time of N in the ecosystem. This is a lower-bound estimate of the catchment-wide PN erosion rate over a few years in the Liwu and Wulu River catchments, where most of the soil and vegetation samples have been collected (Sect. 2). Due to the expected relationship between $k_{\rm F}$ and slope for overland flow processes (Dietrich et al., 2003), 15 the mass balance model predicts a negative correlation between $\delta^{15}N$ and slope, which is consistent with the soil and plant data from Taiwan (Fig. 3, Tables 1 and 2).

The isotopic signature of the N loss processes which cause fractionation have not been assessed in Taiwan (Kao et al., 2004; Huang et al., 2012). However, we note that $\alpha_{\rm f} = 0.994$ is well within the published range of values (Handley and Raven, 1992;

- ²⁰ that $a_f = 0.994$ is well within the published range of values (Handley and Raven, 1992; Brenner et al., 2001). If gaseous loss occurs under anaerobic conditions in waterlogged soils (e.g. Houlton et al., 2006) then k_f may decrease on steeper parts of the landscape as modelled by the " k_{ex} constant" scenario described above (Fig. 5). However, increased solute leaching with increasing slope could have the opposite effect on
- $k_{\rm f}$, and high rates of dissolved N loss have been observed in mountain forest elsewhere (Brookshire et al., 2012a). Given the present uncertainty in the behaviour of $k_{\rm f}$ in this landscape, we also model a scenario where $k_{\rm f}$ remains constant at $1 \times 10^{-3} \, {\rm yr}^{-1}$, while



(5)

 $k_{\rm E}$ increases from 0 yr⁻¹ to 1 × 10⁻³ yr⁻¹ (i.e. " $k_{\rm ex}$ variable"). This produces a negative reciprocal relationship between $k_{\rm E}$ and ecosystem δ^{15} N (Fig. 5). A reciprocal trend between δ^{15} N and slope is also consistent with the soil ($r^2 = 0.35$; P < 0.0001) but not the plant data ($r^2 = 0.12$; P = 0.07) data. In this case it is difficult to model the observed variability in δ^{15} N values, and the " $k_{\rm ex}$ constant" scenario describes better the first order pattern in the data (Fig. 3). This further supports the hypothesis of marked heterogeneity in the source of dissolved N loss from some ecosystems (Hedin et al., 2009; Brookshire et al., 2012a) and extends it to PN loss pathways (Fig. 5). It also implies that fractionating losses may decrease where PN loss dominates export, a geomorphic control on inorganic N that warrants further investigation.

5.3 A common geomorphic control on δ^{15} N

The mass balance model demonstrates that the range in soil δ^{15} N of Taiwanese forest may be explained by variation of the relative importance of fractionating versus nonfractionating N loss across the mountain landscape (Fig. 5). The negative relationship between soil and plant δ^{15} N values and topographic slope (Fig. 3) is consistent with an increase in soil erosion and PN loss with increasing slope (Dietrich et al., 2003). This process-based explanation should not be unique to Taiwan, but also affect other mountain forest ecosystems around the world. To date, many ecological studies using δ^{15} N have attempted to eliminate slope as an environmental variable when collecting soil and plant samples (e.g. Martinelli et al., 1999; Houlton et al., 2006). In contrast, 20 Townsend-Small et al. (2005) applied a sampling strategy similar to ours, collecting bulk soils and plant organic matter along an elevation transect in the Peruvian Andes. They reported a large range in soil and plant δ^{15} N values, with no significant link between $\delta^{15}N$ and temperature (elevation). We reinterpret their data with additional measurements of the local slope at sample sites obtained from the SRTM digital elevation model (90 × 90 m grid). Further, we also consider published soil data from Marin



County, California, where the inverse of slope angle (a proxy for residence time) was used to explain variability in soil δ^{15} N (Amundson et al., 2003).

The Peruvian and Californian soil data are broadly consistent with the findings from Taiwan (Fig. 6). The Californian data exhibit a significant negative correlation between slope and $\delta^{15}N$ (P = 0.007, n = 14) which is stronger than that reported for the inverse of slope (Amundson et al., 2003). On slopes steeper than $\sin \theta = 0.35$, the Peruvian soil data (Townsend-Small et al., 2005) also exhibit a significant negative correlation between slope and $\delta^{15}N$ (P = 0.004, n = 7). Plant samples from multiple species also mirror this trend (P = 0.05, n = 6). Like Taiwan, both locations experience tectonic convergence, which builds steep topography and promotes high physical erosion rates (Bren-

- ner et al., 2001; Townsend-Small et al., 2008). However, on slopes with $\sin \theta < 0.35$ the link between soil and plant δ^{15} N values and slope is not significant in the Andean forest (Fig. 6). In headwater catchments of the Andes, physical erosion rates have been estimated at 0.2–0.4 mmyr⁻¹ (Safran et al., 2005), 10–20 times lower than those of the
- ¹⁵ Central Range, Taiwan (Dadson et al., 2003). We infer that, as a consequence, $k_{\rm E}$ only becomes significant for the N mass balance on the steepest slopes of this forest with the highest erosion rates (sin $\theta > 0.35$). On shallower slopes (angle < 21°), variability in pathways of fractionating loss ($k_{\rm f}$ and $\alpha_{\rm f}$) controls δ^{15} N values as it is thought to do elsewhere (e.g. Houlton et al., 2006). Nevertheless, the commonality of our findings ²⁰ (Fig. 3) and the Peruvian and Californian data (Fig. 6) suggests that PN removal by
- ²⁰ (Fig. 3) and the Peruvian and Californian data (Fig. 6) suggests that PN removal by physical erosion and its export by mountain rivers can set soil δ^{15} N and is a major loss term in the N cycle of mountain forests.

This PN loss provides a strong coupling between climate and N cycling, which has not previously been recognised (Amundson et al., 2003). It arises because physical erosion rates in mountain forest are closely linked to the amount and variability of precipitation and runoff (Dadson et al., 2003; Milliman and Farnsworth, 2011; Hilton et al., 2012). Our findings suggest that a change to a wetter and/or stormier, more erosive climate may impact the N cycle of forest by enhanced PN loss. However, in Taiwan this effect is subsumed at present by significant anthropogenic N inputs, which



exceed PN export by physical erosion, explaining the combination of high N export rates and inferred N rich conditions in this ecosystem (Kao et al., 2004). Under natural conditions, PN export may reinforce the coupling of N cycling and climate, providing a broader context and motivation for further studies on the impact of erosion on N cycling in mountain forest at the catchment scale.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/12593/2012/ bgd-9-12593-2012-supplement.pdf.

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Table 1. Correlation matrix (Pearson) for soil samples $(n = 13)$ from the Central Range, Taiwan.
Values in bold are different from 0 with a significance level $\alpha = 0.05$, P values are given in
parentheses.

Variables	MAT (°C)	MAP (mm)	Slope (sin θ)	C/N	¹⁴ C age (yr)
MAP (mm)	-0.60	_			
Slope (sin θ)	0.63	-0.11 (0.72)	-		
C/N	0.39	-0.22	0.11	-	
¹⁴ C age (yr)	(0.19) -0.48 (0.09)	(0.40) 0.07 (0.81)	-0.45 (0.12)	-0.83 (0.0004)	-
δ^{15} N (‰)	-0.70 (0.008)	0.52 (0.067)	-0.62 (0.025)	-0.17 (0.58)	-0.26 (0.39)



Table 2. Correlation matrix (Pearson) for <i>Pinus morrisonicola</i> and <i>Cymbopogon</i> sp. $(n = 23)$
from the Central Range, Taiwan. Values in bold are different from 0 with a significance level
α = 0.05, <i>P</i> values are given in parentheses.

Variables	MAT (°C)	MAP (mm)	Slope (sin θ)	C/N
MAP (mm)	-0.70 (0.0002)	_		
Slope (sin θ)	0.29 (0.34)	-0.07 (0.76)	-	
C/N	0.4Ó	-0.32	0.23	_
	(0.06)	(0.14)	(0.29)	
δ ¹⁵ N (‰)	-0.11 (0.62)	0.18 (0.42)	–0.59 (0.003)	-0.25 (0.24)





Fig. 1. Controls on the bulk δ^{15} N of a forest ecosystem with external N input and output (black arrows) and internal N cycling (grey arrows). The isotopic ratio of external inputs (R_{ex}) delivered at a rate I_{ex} (tN km⁻² yr⁻¹) are modified by N losses which fractionate N isotopes by a factor α_f (\neq 1) by the rate constant k_f (yr⁻¹). N can also be lost by non-fractioning pathways ($\alpha_E = 1$) which occur at a rate k_E (yr⁻¹). The total N loss rate constant, $k_{ex} = k_f + k_E$.











Fig. 3. Relationship between topographic slope (sin θ) and δ^{15} N of soil (squares) and plants (triangles, *P. morrisonicola* in dark grey and *Cymbopogon* sp. in light grey) from the Central Range, Taiwan. Analytical uncertainty is smaller than the point size. The linear fit to the soil (dashed line) and plant (black line) data are shown with 95% confidence bands shaded grey, returning identical gradients, with soil δ^{15} N=(-8±3)×Slope+(8.0±1.6)‰ and plant δ^{15} N=(-9±3)×Slope+(3.4±1.3)‰.





Fig. 4. C/N and ¹⁴C age for soil organic matter from the Central Range Taiwan. Analytical uncertainty is indicated by grey whiskers if larger than the point size. A mass balance model (black line, Eqs. 1 and 3) describes the first order trend in the data and predicts an integrated average N loss rate constant (k_{ex}) across the dataset, with a minimum misfit parameterisation as shown ($r^2 = 0.63$; P = 0.0006).











Fig. 6. δ^{15} N and slope for soil and plant organic matter from sites in Peru (squares and triangles) and California (diamonds). Lines and shaded region show linear fits to the soil and plant samples from Taiwan (Fig. 3). For the Peruvian data, filled symbols are those where $\sin \theta > 0.35$ (see Sect. 5.3).

