

# An integrated assessment of ecosystem carbon pools and fluxes across an oceanic alpine toposequence

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**Abstract** Alpine ecosystems are predicted to be severely affected by climate change. Cold, wet oceanic-alpine environments may also accumulate large total ecosystem carbon (C) pools, but have rarely been investigated. We assessed C pools and fluxes on a toposequence of oceanic-alpine habitats from blanket mire and boreal *Calluna* heath to *Racomitrium* heath, *Nardus* snowbed and alpine *Calluna* heath. We quantified C pools in vegetation and soils for each habitat and compared these with C inputs from net primary production (NPP) and outputs via decomposition, measured in a 3-year litter bag experiment. We also investigated principle drivers (temperature, moisture, community composition) of C pool and flux differences between habitats. Total ecosystem C pools were large; 11–26 kg C m<sup>-2</sup> in alpine habitats and 50 kg C m<sup>-2</sup> in blanket mire. Within the alpine zone C storage was greatest in the snowbed. Litter decomposition was slow in all habitats ( $k=0.09\text{--}0.29\text{ y}^{-1}$ ) while NPP was within the range reported for continental alpine systems. C pool sizes and C fluxes did not vary consistently with altitude but reflected topographic gradients of tem-

perature and moisture within the alpine zone. Oceanic-alpine ecosystems contain large stores of C which may be vulnerable to the effects of climate change.

**Keywords** Litter decomposition · Primary production · Soil carbon pool · Temperature · Moisture · Altitude

## Introduction

Cold and wet northern biomes contain large stocks of carbon (C) in their soils, and may hold up to one third of the global soil C pool (Mack et al. 2004). Northern high-latitude and altitude areas are also predicted to experience the greatest effects of climate change (Houghton et al. 2001) and indeed there is evidence that rapid warming is already occurring (ACIA 2004; Barnett et al. 2006). The balance between C fixation through primary plant production, and losses resulting from biological, chemical or physical decomposition of plant-derived carbon, determines the rate at which soil C stores are accumulated or depleted. As climate change has the potential to impact on both sides of this equation and thus to change arctic and alpine ecosystems from net sinks of C to net sources (De Deyn et al. 2008; Hagedorn et al. 2010; King et al. 1997), there is an urgent need to understand the factors affecting C fluxes and to quantify the stocks of C held in these ecosystems.

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Alpine ecosystems are frequently considered together with high-latitude systems in terms of ecosystem processes as they have many attributes in common, including low temperatures, a short growing season and a strong influence of climate on plant distributions (Hagedorn et al. 2010). However, alpine ecosystems also have key differences which influence C storage and fluxes, including the interaction between topography and snow cover leading to steep local gradients in soil temperature and moisture, a lack of permafrost, steep slopes resulting in a prevalence of well drained soils and, in many areas, a history of intensive land use (Hagedorn et al. 2010; Seastedt et al. 2001). In contrast to arctic tundra and boreal systems, alpine habitats have been relatively little studied in terms of their C stores and fluxes. In addition, much of the existing information is derived from studies in continental alpine areas, such as the American Rocky Mountains (e.g. Bowman and Seastedt 2001) and European Alps (e.g. Djukic et al. 2010; Körner 1999; Leifeld et al. 2009) while data from oceanic alpine regions are lacking.

Both plant productivity and decomposition rates are generally considered to decline with increasing altitude, due to gradients of decreasing temperature, increasing snowpack duration (and thus shorter growing season) and decreasing vegetation cover (Körner 1999). Studies of soil C stocks along elevation gradients in alpine regions (e.g. Djukic et al. 2010; Garcia-Pausas et al. 2007; Leifeld et al. 2009) have, however, revealed a variety of relationships with altitude, including a decrease (Garcia-Pausas et al. 2007), unimodal response (Djukic et al. 2010) or no change (Garcia-Pausas et al. 2007; Leifeld et al. 2009) in soil C storage with increasing elevation. The variability in relationships between studies demonstrates the likely importance of local variability in climate-altitude relationships and also the scales at which the studies are conducted. A better understanding of the role of local topographic and climatic variability is clearly necessary to predict the impacts of climate change on the C stores held in this biome.

Topographic variability is a major driver of plant productivity and community composition in the alpine zone. The interaction of high topographic diversity and high wind speed results in redistribution of winter snowfall causing steep local gradients of growing season length, soil temperature, moisture and nutrient availability which may persist throughout the year (Seastedt et al. 2004). Consequently, above-

ground plant production has high spatial variability and may vary 10-fold between adjacent communities (Bowman and Fisk 2001). Production generally increases from dry to wet conditions linked to position on the topographic gradient (ridges and hollows respectively, Fisk et al. 1998). This positive effect of soil moisture is related to the positive effect of water availability on nutrient cycling rates (Bowman and Fisk 2001; Fisk et al. 1998) which increases nutrient availability for plant uptake. The positive effect of increased soil moisture in topographic hollows on plant production may, however, be traded off against a reduction in growing season length in locations where snow lies late into the summer (Bowman and Fisk 2001). The variability in growing conditions along topographic gradients in the alpine is also reflected in a high diversity of plant community types (Choler 2005). Plant species vary widely in the amount and quality of the litter which they produce (De Deyn et al. 2008) and, in combination with the variability in production already mentioned, topographic gradients may thus be related to both the magnitude and quality of C inputs to the soil over the long term, which will have a significant influence on ecosystem C storage (Hollingsworth et al. 2008; Jobbágy and Jackson 2000).

The decomposition rate of plant litter determines the residence time of C in the ecosystem C pool before it is lost as gaseous or aqueous emissions such as CO<sub>2</sub>, CH<sub>4</sub> or DOC (Davidson and Janssens 2006). The extensive literature on litter decomposition points to the importance of climate (temperature and moisture), litter quality and the nature of the soil decomposer community for determining rates of litter mass loss across a wide range of ecosystems (Aerts 2006). The relative importance of individual drivers may, however, vary according to the ecosystem under consideration (Murphy et al. 1998; Shaw and Harte 2001; Sjögersten and Wookey 2004). In alpine systems, low temperatures are a major constraint on decomposition rates (Körner 1999). However, as for productivity and species composition, topographic gradients in moisture availability related to snowpack may exert an influence, giving rise to much fine scale variability (Seastedt et al. 2001). Within the alpine zone, decomposition has been shown to peak at intermediate moisture availability (Bryant et al. 1998; O'Lear and Seastedt 1994) and moisture may be the primary constraint on decomposition in xeric

habitats, while temperature is more limiting in mesic habitats (Seastedt et al. 2001). Alpine species also differ widely in the quality of the litter which they produce, with differences between forbs, graminoids and shrubs being especially pronounced (De Deyn et al. 2008). Changes in species composition along topographic gradients and the resulting changes in litter quality will interact with the direct effects of temperature and moisture on decomposition rates to reinforce the high degree of spatial variability in outputs from the ecosystem C pool.

Given the importance of climate for determining C fluxes within the alpine and the wide range of climatic zones within which alpine ecosystems occur, there is a clear need for studies of C fluxes and pools across a broad range of alpine areas. Oceanic alpine areas are characterised by lower annual temperature variation and higher rainfall than their continental counterparts—both factors which could significantly affect the storage and fluxes of C. In this study we set out to characterise plant and soil C pools, net primary production (NPP) and decomposition rates across a typical toposequence of oceanic alpine habitats, including the three most prevalent alpine habitats in the UK (representative of oceanic alpine habitats in large parts of Europe). Following on from this, we examined how differences between habitats in terms of C storage and fluxes were related to key environmental differences and plant species composition and also the relationships between C pools and fluxes of C in NPP and decomposition. We aimed to test three initial hypotheses: (1) that NPP declines with altitude (2) that decomposition is determined primarily by litter quality and temperature; moisture not being limiting in an oceanic alpine environment and (3) that total ecosystem C pool size varies on a habitat-specific basis as a result of interactions between NPP and decomposition.

## Materials and methods

### Study area

The Allt a'Mharcaidh catchment (3°50' W, 57°5' N; Fig. 1) is located on the western edge of the Cairngorm Mountains in the eastern Highlands of Scotland. It covers an area of around 10 km<sup>2</sup>, spans an altitudinal range of 320 m to 1111 m and is underlain by granite. The climate is cool oceanic with

mean monthly temperatures (at 575 m) ranging from 1.2°C in February to 10.3°C in July, and mean annual rainfall of around 1100 mm, approximately 30% of which falls as snow in winter (Helliwell et al. 1998). The catchment represents a typical Scottish upland/alpine ecosystem with blanket mire vegetation on deep peat soils in the valley bottom, lichen-rich heather (*Calluna vulgaris*) moor and podzolic soils on the valley sides and a high plateau with alpine soils and vegetation above 700 m.

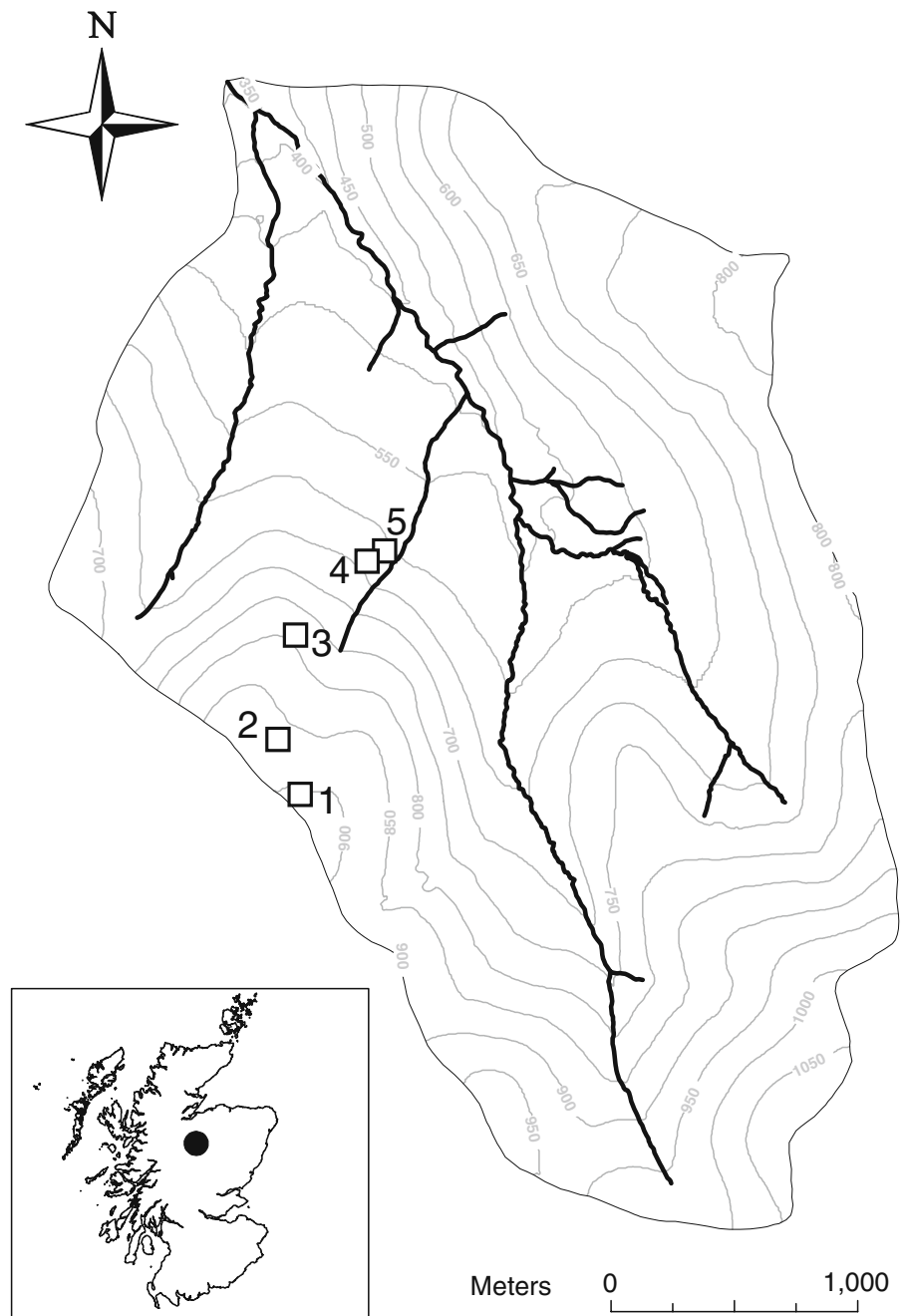
In this study, a contiguous toposequence of 5 plant communities on a north east facing slope (Fig. 1) was selected to be representative of the main boreal and alpine habitats present in the catchment and more widely in oceanic alpine areas. These were, in order of increasing altitude: blanket mire, boreal *Calluna* heath 'boreal heath', alpine *Calluna* heath 'alpine heath', *Nardus stricta*-dominated snowbed 'snowbed' and *Racomitrium lanuginosum* moss heath 'Racomitrium heath' (details in Table 1; species names abbreviated to genus from this point for convenience). In each habitat, vegetation and soils were characterised as described below, including; above and below ground plant biomass and chemistry, litter chemistry and decomposition rate, soil profile and chemistry and measurements of soil temperature and moisture.

### Vegetation sampling

Vegetation biomass both above and below ground was sampled at peak biomass in mid-August 2005, before the onset of senescence in deciduous species. Grazing levels are extremely low in the catchment so protection of plots from grazing was not considered necessary. In each habitat biomass was sampled in five 50 cm×50 cm quadrats. All above ground biomass (AGB) including attached dead material was collected by clipping the vegetation at the soil surface. The underlying litter layer, including L and LF horizons, was collected and stored separately. After removal of the litter layer, 3 cores (3.5 cm diameter×depth of visible rooting, maximum 21 cm) were taken in each quadrat for determination of below ground biomass (BGB). All biomass samples and cores were stored frozen at -20°C until processing.

Fresh weight of AGB and litter layer samples was recorded prior to sorting and where AGB was large (snowbed, boreal heath and blanket mire; Table 1 and 2) a random sub-sample of around 25% was taken. For all

**Fig. 1** Location of the Allt a'Mharcaidh catchment and toposequence study sites



habitats, AGB was sorted into lichen, moss, graminoid, herb and shrub. Mosses were then further split into green (photosynthetic) and brown (non photosynthetic but still living) material; graminoids into current year leaves and flowering stems vs. attached dead material and stem bases; and shrubs into current year shoot increments vs. older material and woody shoots. The three BGB cores from each quadrat were pooled and

any additional litter was removed from the upper layers before the roots were washed out of the soil.

After sorting, all material was dried at 60°C for at least 48 hours and dry weight was recorded. A 2–3 g sub-sample of each biomass fraction was then ball milled and total C and N content was measured using a Flash EA1112 Elemental Analyser (ThermoFinnigan, Milan, Italy). C content data was then used to calculate

**Table 1** Characteristics of toposquence sampling sites. Temperature data are for the period November 2004 to October 2007, winter is November to April and summer is May to October. Soil temperature and moisture data are from measurements at each site, air temperature data are from the Environmental Change Network monitoring site at an altitude of 700 m, approximately 2 km from the study area. NVC code refers to the British National Vegetation Classification (Rodwell 1991, 1992). Soil types are named according to both the Scottish and World Reference Base for Soil Resources (WRB) soil classifications; no. soil profiles used indicates the total number of profiles used in estimating soil C pools for each habitat type. Temperature and moisture values are means of seasonal means ( $n=3$ ) derived from hourly measurements  $\pm$  SD. Within rows, means not sharing the same letter are significantly different ( $P<0.05$ )

| Habitat                           | Blanket mire  | Boreal heath                                      | Alpine heath                                     | Snowbed   | Racomitrium heath   |
|-----------------------------------|---|---|--|---|---|
| Vegetation type                   | <i>Calluna vulgaris-Eriophorum vaginatum</i> blanket mire | <i>Calluna vulgaris-Vaccinium myrtillus</i> heath | <i>Calluna vulgaris-Cladonia arbuscula</i> heath | <i>Nardus stricta-Carex bigelowii</i> grass heath | <i>Carex bigelowii-Racomitrium lanuginosum</i> moss heath |
| NVC code                          | M19   | H12/H21   | H13  | U7  | U10   |
| Mean graminoid + herb cover (%)   | 40  | 3   | 1  | 52  | 2   |
| Mean shrub cover (%)              | 45  | 41  | 56   | 15  | 8   |
| Mean bryophyte cover (%)          | 38  | 3   | 2  | 35  | 82  |
| Mean lichen cover (%)             | 13  | 81  | 18   | 9   | 11  |
| Altitude (m)                      | 621   | 640   | 794  | 882   | 908   |
| Slope (°)                         | 16  | 16  | 18   | 10  | 8   |
| Aspect (°)                        | 62  | 55  | 53   | 26  | 0   |
| Soil type (Scottish/WRB)          | Dystrophic peat/Sapric histosol (dystric)                 | Peaty podzol/Stagnic histic podzol                | Oroarctic podzol/Endoskeletal podzol             | Peaty podzol/Histic podzol                        | Oroarctic podzol/Endoskeletal podzol                      |
| No. soil profiles used            | 10  | 12  | 14   | 2   | 9   |
| Mean summer air temp (°C)         | –   | –   | 8.86 $\pm$ 1.29                                  | –   | –   |
| Mean winter air temp (°C)         | –   | –   | 1.79 $\pm$ 0.96                                  | –   | –   |
| Mean summer soil temp (°C)        | 8.67 $\pm$ 0.53 bc  | 9.49 $\pm$ 0.34 c                                 | 8.59 $\pm$ 0.86 bc                               | 8.03 $\pm$ 0.34 ab                                | 7.23 $\pm$ 0.53 a   |
| Mean winter soil temp (°C)        | 3.15 $\pm$ 0.60 b   | 1.96 $\pm$ 0.48 a                                 | 1.29 $\pm$ 0.68 a                                | 1.13 $\pm$ 0.48 a                                 | 0.91 $\pm$ 0.59 a   |
| Mean summer soil moisture (%vol)  | 66.1 $\pm$ 0.5 c  | 60.1 $\pm$ 2.8 b                                  | 22.3 $\pm$ 0.6 a                                 | 67.3 $\pm$ 0.3 c                                  | 59.6 $\pm$ 4.4 b  |
| Mean winter soil moisture (%vol)  | 66.9 $\pm$ 0.6 c  | 63.6 $\pm$ 2.4 c                                  | 22.7 $\pm$ 0.7 a                                 | 65.9 $\pm$ 0.3 c                                  | 54.7 $\pm$ 8.0 b  |
| Mean growing degree days (>5°C)   | 697 $\pm$ 83 bc   | 854 $\pm$ 115 c                                   | 700 $\pm$ 139 bc                                 | 584 $\pm$ 76 ab                                   | 459 $\pm$ 85 a  |
| Mean hours of frost (<0°C)        | 0 $\pm$ 0   | 699 $\pm$ 880                                     | 1445 $\pm$ 959                                   | 844 $\pm$ 1442                                    | 1669 $\pm$ 1195   |
| Mean growing season length (days) | 203 $\pm$ 10 b  | 198 $\pm$ 13 b                                    | 185 $\pm$ 20 ab                                  | 173 $\pm$ 23 ab                                   | 156 $\pm$ 19 a  |

**Table 2** Vegetation productivity, ecosystem C pools and initial litter characteristics in the five habitat types. Values are means  $\pm$  SEM. Within rows, means not sharing the same letter are significantly different ( $P < 0.05$ ). Above ground NPP values exclude production by lichens.

| Habitat  | Blanket mire       | Boreal heath        | Alpine heath        | Snowbed            | <i>Racomitrium</i> heath |
|--|--------------------|---------------------|---------------------|--------------------|--------------------------|
| Above ground NPP (g C m <sup>-2</sup> y <sup>-1</sup> excl. lichens) | 165 $\pm$ 30 b     | 73 $\pm$ 5 a        | 53 $\pm$ 5 a        | 93 $\pm$ 7 a       | 66 $\pm$ 6 a             |
| % NPP from graminoids + herbs  | 8                  | 27                  | 0                   | 40                 | 13                       |
| % NPP from shrubs  | 54                 | 69                  | 97                  | 44                 | 12                       |
| % NPP from bryophytes  | 38                 | 4                   | 3                   | 16                 | 75                       |
| Above ground biomass C pool (kg m <sup>-2</sup> )                    | 1.45 $\pm$ 0.35 b  | 0.73 $\pm$ 0.04 a   | 0.45 $\pm$ 0.02 a   | 0.49 $\pm$ 0.04 a  | 0.59 $\pm$ 0.12 a        |
| Belowground biomass C pool (kg m <sup>-2</sup> )                     | 0.23 $\pm$ 0.07 b  | 0.16 $\pm$ 0.01 ab  | 0.26 $\pm$ 0.07 b   | 0.31 $\pm$ 0.06 b  | 0.06 $\pm$ 0.02 a        |
| Litter C pool (kg m <sup>-2</sup> )                                  | 0.98 $\pm$ 0.24 c  | 0.65 $\pm$ 0.05 abc | 0.26 $\pm$ 0.06 a   | 0.48 $\pm$ 0.18 ab | 0.89 $\pm$ 0.12 bc       |
| Soil C pool (kg m <sup>-2</sup> )                                    | 47.18 $\pm$ 3.30 c | 18.73 $\pm$ 2.74 ab | 13.25 $\pm$ 1.52 ab | 24.86 $\pm$ 1.86 b | 9.94 $\pm$ 3.98 a        |
| % total C pool in soil   | 95                 | 92                  | 94                  | 95                 | 87                       |
| % total C pool in organic soil horizons                              | 92                 | 42                  | 9                   | 61                 | 7                        |
| % total C pool in mineral soil horizons                              | 3                  | 50                  | 85                  | 34                 | 80                       |
| Litter C:N   | 49.6 $\pm$ 0.8 b   | 67.7 $\pm$ 3.0 c    | 41.1 $\pm$ 0.8 a    | 43.7 $\pm$ 1.8 ab  | 84.5 $\pm$ 4.6 d         |
| Litter N:P   | 24.1 $\pm$ 3.8 a   | 24.4 $\pm$ 3.1 a    | 30.4 $\pm$ 3.7 a    | 42.7 $\pm$ 8.8 a   | 29.9 $\pm$ 6.7 a         |
| Litter % N   | 1.01 $\pm$ 0.01 c  | 0.75 $\pm$ 0.03 b   | 1.23 $\pm$ 0.02 d   | 1.04 $\pm$ 0.05 c  | 0.54 $\pm$ 0.03 a        |
| Litter decomposition rate k (proportion lost y <sup>-1</sup> )       | 0.268              | 0.175               | 0.175               | 0.295              | 0.090                    |

C pool sizes (kg m<sup>-2</sup>) for each biomass fraction. Above ground Net Primary Production (NPP) was determined as the sum of current year graminoid and shrub fractions plus a proportion of the green moss fraction. The proportion of green moss derived from current year growth was calculated using a shoot extension rate of 4.5 mm y<sup>-1</sup> for *R. lanuginosum* (Armitage 2010) and 10 mm y<sup>-1</sup> for *Sphagnum* (Aerts et al. 1992) coupled with measurements of green shoot lengths in the biomass samples. This suggested that, for both species, the total green moss biomass represented approximately 6 years growth. Estimates of NPP excluded C fixation by lichens since no suitable growth rate data were available for this group.

#### Litter decomposition

Litter decomposition rates were measured over a 3 year period (2004–07) using surface-placed litter bags collected every 6 months (6 harvests). Fresh litter was collected by hand from each of the 5 habitats along the toposequence in October 2004, at the time of senescence. Collecting was done over a large area within each habitat type to ensure adequate representation of all species and plant parts. In the case of *Racomitrium* heath, higher plant litter was extremely scarce and bryophytes dominated the AGB

so sections of the moss mat were collected and 1 cm sections of brown senescent shoot material from immediately below the green part of the shoots were used in addition to the vascular plant litter. All litter was removed to the laboratory and any green or non-senescent material and seeds or seed heads were removed. Large pieces of litter were cut into 5 cm sections and smaller pieces cut in half. The material was then air dried at room temperature to a constant weight (3–4 days). 60 litter bags (6 harvests  $\times$  10 replicates) were prepared for each habitat, using 10  $\times$  8 cm bags made from 1 mm polypropylene mesh. The litter was sorted into shrub, graminoid/herb and moss material and weighed to determine the relative amounts of each to be added to the litter bags, totalling approximately 1 g of mixed, air dried litter from the appropriate habitat in each bag. In the case of *Racomitrium* heath, a 75:25 mixture of moss litter and higher plant material was used. Five additional 1 g samples of litter from each habitat were retained for determination of air dry/oven dry mass ratio and initial litter chemistry (see below).

The litter bags were installed at the field site in November 2004, placed back into their respective habitats, pinned to the soil (or moss mat) surface, ensuring good contact between the soil and the litter. Bags were placed randomly in 10 groups of 6 in each



habitat and sections of plastic mesh were placed over the top to prevent disturbance by wind or animals during incubation.

Following incubation, 10 bags were collected from each habitat at 6 monthly intervals, in May and November of each year, representing alternate summer and winter periods. Following collection, the bags were immediately opened and the contents sorted, removing any visible plant roots, soil animals and soil particles. The remaining litter was oven dried at 60°C for 3 days, its dry weight recorded and then ball milled prior to chemical analysis. The ground litter samples were analysed for total C and N content as above and total phosphorus (P) was determined by digestion in concentrated sulphuric acid with a selenium catalyst followed by ICP-AES (Iris inductively coupled plasma-atomic emission spectrometer, Thermo-Jarrell Ash, Franklin, MA).

### Soil sampling

In each habitat, a soil pit was excavated to a depth below the last soil horizon that exhibited clear changes due to pedogenesis and into the underlying parent material, around 1 m depth. Each horizon was identified, classified and described according to standard Soil Survey of Scotland procedures (Miller et al. 1999). A soil sample of approximately 1.5 kg was taken from the middle of each of the main horizons within the profile and subsequently prepared for analysis by air drying at 30°C and sieving to remove stones and particles >2 mm. A 2–3 g sub-sample was then ball milled and oven dried at 50°C before total C and nitrogen (N) content was measured using an elemental analyser. Soil cores of fixed volume were also taken from each soil layer where possible, to determine soil bulk density. Cores were either taken in triplicate in rings of 210 cm<sup>3</sup> or singly in rings of 667 cm<sup>3</sup> depending on the thickness and stoniness of the horizon. The contents of the rings were oven dried at 105°C for 48 h and sieved (2 mm sieve) to remove stones before weighing to determine bulk density.

The soil C pool (kg m<sup>-2</sup>) was calculated for each horizon (as the product of C content, bulk density and horizon thickness) and then adjusted for the volume of large stones not accounted for in the bulk density cores using information on horizon stone content from the profile description. The C pool in each horizon was then summed to give an estimate of the total soil pool per unit area. To ensure soil C pool

estimates were representative of the habitats, data from the toposequence sites was supplemented with data from earlier samplings of the same plant community/soil type combinations (mainly within the Allt a'Mharcaidh catchment; see Table 1 for number of profiles used) held on the Scottish Soils Database. Data on C content of each horizon and profile descriptions were extracted and used to calculate C pools as above. Where horizon bulk density information was missing from the database profiles, mean horizon bulk densities from the corresponding soil type/plant community combinations on the toposequence were used in the calculations.

### Environmental drivers

Hourly measurements of soil temperature (107 temperature probe, Campbell Scientific, Loughborough, UK) and volumetric moisture content (Theta probe, Delta-T instruments, Cambridge, UK) at 10 cm depth in the organic soil horizon were made from November 2004–November 2007 at four replicate locations within each habitat (20 locations in total). The hourly temperature and moisture data were used to calculate a number of metrics describing environmental conditions in each habitat. Mean annual temperature and moisture was calculated along with mean seasonal values representing the summer (May to October) and winter (November to April) periods used in the litter decomposition study (Table 1). Temperature data were also used to calculate annual growing degree days ( $GDD = \sum (\text{daily mean temperature} - 5)$  for all days when mean temperature >5°C), freezing hours (FH = annual number of hours for which mean temperature <0°C) and growing season length (GSL = period (days) bounded by daily mean temperature >5°C and <5°C (after 1<sup>st</sup> July) for ≥6 days).

Mean cover of each of the major plant functional types (i.e. shrubs, graminoids, herbs, bryophytes and lichens) was determined for each habitat along the toposequence during a vegetation survey in August 2005. Ten 1 m×1 m quadrats were placed randomly in each habitat type and percentage cover of all plant species present was recorded.

### Data analysis

Temperature and moisture differences between habitat types were analysed using one-way analysis of

variance of annual values, while relationships between temperature and moisture variables and altitude were examined using linear and non-linear regression across all five habitats. Analysis of variance was also used to examine between-habitat differences in biomass C pools, soil C pools, litter quality and litter mass loss. Mean data on biomass and soil C pools were then combined to give a single estimate of mean total ecosystem C pool size for each habitat. Linear and non-linear regression was used to explore inter-relationships between productivity, decomposition, litter quality, environmental variables and C pool sizes and ratios at the between-habitat level ( $n=5$ ) to give an indication of potential controls on C pools and fluxes. All analyses were carried out using Genstat v 11.1. Where necessary, the data were transformed before analysis to ensure normality; in the litter bag study percentage nutrient content data were arcsine transformed before analysis and percentage mass loss data were transformed using  $\ln[(1+x)/(1-x)]$ .

## Results

### Environmental gradients

Soil temperature declined with increasing altitude under both summer and winter conditions (Table 1). Mean annual soil temperature exhibited a lapse rate of  $5.7^\circ\text{C}/1000\text{ m}$  ( $R^2=0.95$ ;  $F_{1,14}=280.07$ ;  $P<0.001$ ) giving a temperature difference of  $1.8^\circ\text{C}$  between the top and bottom of the slope (908 m and 621 m respectively). The lapse rate was found to vary seasonally, being steeper in winter ( $6.3^\circ\text{C}/1000\text{ m}$ ) than in summer ( $5.3^\circ\text{C}/1000\text{ m}$ ) because soil temperature in the blanket mire was  $1^\circ\text{C}$  warmer in winter and  $1^\circ\text{C}$  cooler in summer than predicted by its altitude. Seasonal variation in temperature within habitats was greater than variation between habitats along the toposequence. The magnitude of seasonal (summer-winter) variation decreased with altitude from  $7.5^\circ\text{C}$  in the boreal heath to  $6.3^\circ\text{C}$  in the *Racomitrium* heath; the blanket mire was the exception to this pattern, having a low seasonal variation of  $5.5^\circ\text{C}$ . Growing season length declined with altitude (Table 1;  $R^2=0.50$ ;  $F_{1,14}=14.82$ ;  $P=0.002$ ) as did GDD (Table 1;  $R^2=0.46$ ;  $F_{1,14}=13.01$ ;  $P=0.003$ ). Freezing hours showed high variability between years, but increased rapidly up the slope from the blanket mire to the alpine heath (Table 1). Within the three alpine

habitats soil freezing occurred much less in the snowbed than in the alpine heath and *Racomitrium* heath. Volumetric soil moisture content also differed significantly between habitats (Summer:  $F_{4,14}=180.97$ ,  $P<0.001$ ; Winter:  $F_{4,14}=72.48$ ,  $P<0.001$ ; Table 1). Alpine heath had the driest soil by far (mean 22%vol.) while the blanket mire and snowbed experienced permanently wet conditions (mean 66–67%vol.). *Racomitrium* heath and boreal heath habitats were intermediate, with mean soil moisture content ranging from 55–64%vol.

### Above ground NPP

The amount of carbon fixed in above ground NPP varied significantly between habitats ( $F_{4,24}=8.93$ ,  $P<0.001$ ; Table 2) but this was driven by the difference between blanket mire ( $165\text{ gC m}^{-2}\text{ y}^{-1}$ ) and the other habitats ( $53\text{--}93\text{ gC m}^{-2}\text{ y}^{-1}$ ). Within the alpine habitats NPP was greatest in the snowbed and least in the alpine heath, though productivity of these communities was not significantly lower than in the boreal heath (Table 2). The contribution of different plant groups to NPP varied greatly between the habitats (Table 2) reflecting the differences in community composition (Table 1). When mean NPP for each habitat was correlated with seasonal mean soil temperature and moisture variables, GSL, GDD, FH, altitude and mean cover of the main plant groups (Table 3), a significant negative relationship was found between NPP and FH ( $\text{NPP}=145-0.06*\text{FH}$ ;  $R^2=0.70$ ;  $F_{1,4}=10.28$ ;  $P=0.049$ ). None of the other tested variables had individually significant relationships with NPP.

### Biomass C pools

AGB C pools (Table 2; Fig. 2a) followed a similar pattern to NPP with the exception that standing biomass in the snowbed was lower than NPP might have suggested, possibly due to the high proportion of graminoids and minimal build up of woody material. The contribution of different plant groups to the AGB C pool varied greatly between habitats (Fig. 2a). The amount of C in shrub biomass declined with altitude, while lower plants formed a significant part of the AGB C pool in all habitats; mosses were most important in *Racomitrium* heath, snowbed and blanket mire, while lichens were dominant in alpine and boreal heath. BGB C pools were relatively small compared to

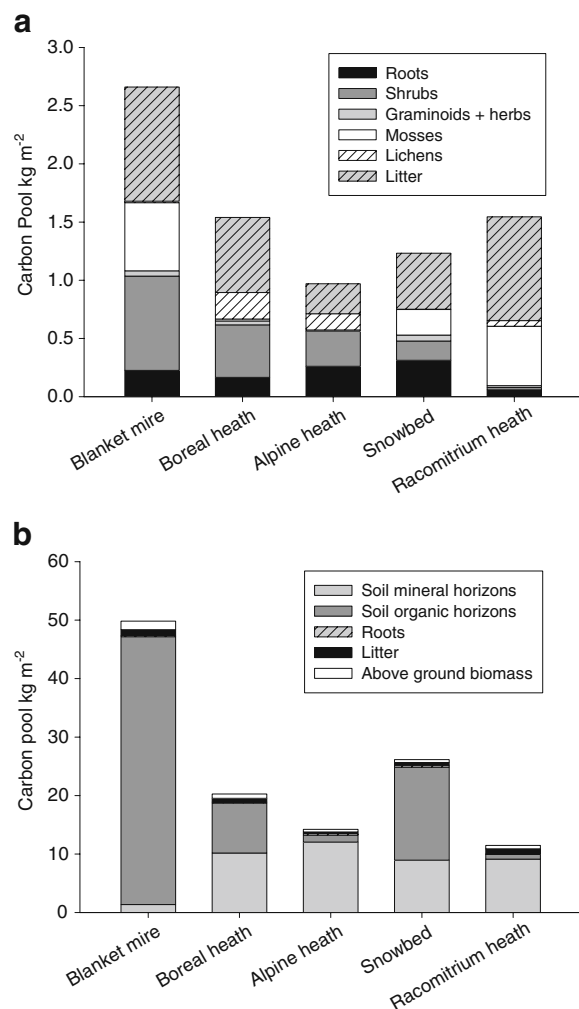


**Table 3** Inter-correlations between C pool sizes and habitat traits. Correlation co-efficients are shown, those in bold are significant at  $P=0.05$  or less,  $n=5$  for all variables

|                      | ABG C pool   | BGB C pool | Litter C pool | Soil C pool   | TE C pool     | Altitude      | MST          | MWT           | MAT          | MSM          | MWM          | MAM    | GDD          | GSL    | FH            | NPP    | k            | Bryo. cover | Shrub cover | Gram. cover | Bryo. + lichen cover |  |
|----------------------|--------------|------------|---------------|---------------|---------------|---------------|--------------|---------------|--------------|--------------|--------------|--------|--------------|--------|---------------|--------|--------------|-------------|-------------|-------------|----------------------|--|
| AGB C pool           |              |            |               |               |               |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| BGB C pool           | -0.014       |            |               |               |               |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| Litter C pool        | 0.732        | -0.575     |               |               |               |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| Soil C pool          | <b>0.888</b> | 0.410      | 0.479         |               |               |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| TE C pool            | <b>0.898</b> | 0.389      | 0.497         | <b>0.999</b>  |               |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| Altitude             | -0.731       | -0.093     | -0.282        | -0.619        | -0.622        |               |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| MST                  | 0.287        | 0.304      | -0.206        | 0.296         | 0.291         | -0.851        |              |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| MWT                  | <b>0.946</b> | 0.161      | 0.511         | <b>0.882</b>  | <b>0.886</b>  | <b>-0.894</b> | 0.571        |               |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| MAT                  | 0.710        | 0.259      | 0.188         | 0.677         | 0.677         | <b>-0.985</b> | 0.876        | <b>0.896</b>  |              |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| MSM                  | 0.443        | -0.155     | 0.702         | 0.479         | 0.487         | -0.109        | -0.122       | 0.299         | 0.109        |              |              |        |              |        |               |        |              |             |             |             |                      |  |
| MWM                  | 0.494        | -0.094     | 0.667         | 0.538         | 0.544         | -0.251        | 0.045        | 0.398         | 0.257        | <b>0.986</b> |              |        |              |        |               |        |              |             |             |             |                      |  |
| MAM                  | 0.470        | -0.125     | 0.687         | 0.511         | 0.518         | -0.181        | -0.038       | 0.349         | 0.184        | <b>0.996</b> | <b>0.996</b> |        |              |        |               |        |              |             |             |             |                      |  |
| GDD                  | 0.256        | 0.272      | -0.223        | 0.248         | 0.244         | -0.840        | <b>0.998</b> | 0.543         | 0.859        | -0.161       | 0.004        | -0.078 |              |        |               |        |              |             |             |             |                      |  |
| GSL                  | 0.631        | 0.381      | 0.036         | 0.644         | 0.641         | <b>-0.953</b> | <b>0.902</b> | 0.848         | <b>0.986</b> | -0.020       | 0.132        | 0.056  | <b>0.885</b> |        |               |        |              |             |             |             |                      |  |
| FH                   | -0.829       | -0.393     | -0.406        | <b>-0.934</b> | <b>-0.933</b> | 0.777         | -0.561       | <b>-0.902</b> | -0.832       | -0.529       | -0.631       | -0.581 | -0.517       | -0.791 |               |        |              |             |             |             |                      |  |
| NPP                  | <b>0.921</b> | 0.255      | 0.629         | <b>0.980</b>  | <b>0.983</b>  | -0.542        | 0.146        | 0.850         | 0.578        | 0.569        | 0.602        | 0.587  | 0.099        | 0.519  | <b>-0.880</b> |        |              |             |             |             |                      |  |
| k                    | 0.392        | 0.843      | -0.071        | 0.768         | 0.755         | -0.282        | 0.277        | 0.476         | 0.429        | 0.361        | 0.420        | 0.392  | 0.224        | 0.469  | -0.753        | 0.673  |              |             |             |             |                      |  |
| Bryo. cover          | 0.093        | -0.561     | 0.652         | -0.045        | -0.031        | 0.537         | -0.869       | -0.234        | -0.608       | 0.478        | 0.333        | 0.407  | -0.875       | -0.710 | 0.259         | 0.148  | -0.283       |             |             |             |                      |  |
| Shrub cover          | 0.297        | 0.369      | -0.329        | 0.268         | 0.262         | -0.706        | 0.760        | 0.538         | 0.727        | -0.597       | -0.473       | -0.537 | 0.769        | 0.810  | -0.334        | 0.126  | 0.155        | -0.801      |             |             |                      |  |
| Gram. cover          | 0.363        | 0.651      | 0.147         | 0.716         | 0.707         | -0.009        | -0.092       | 0.319         | 0.137        | 0.585        | 0.583        | 0.586  | -0.148       | 0.140  | -0.628        | 0.695  | <b>0.914</b> | 0.118       | -0.228      |             |                      |  |
| Bryo. + lichen cover | 0.081        | -0.855     | 0.655         | -0.223        | -0.205        | -0.007        | -0.153       | -0.066        | -0.121       | 0.574        | 0.542        | 0.560  | -0.141       | -0.273 | 0.097         | -0.086 | -0.532       | 0.512       | -0.551      | -0.323      |                      |  |

Abbreviations are as follows: *AGB* Above ground biomass, *BGB* Below ground biomass, *TE* Total ecosystem, *MST* Mean summer soil temperature, *MWT* Mean winter soil temperature, *MAT* Mean annual soil temperature, *MSM* Mean summer soil moisture, *MWM* Mean winter soil moisture, *MAM* Mean annual soil moisture, *GDD* Growing degree days, *GSL* Growing season length, *FH* Frost hours, *NPP* Net primary productivity, *k* Litter decomposition rate, *Bryo.* Bryophyte, *Gram.* Graminoid. See text for derivation of variables

above ground pools (Table 2; Fig. 2a) but this was partly due to the dominance of lower plants. When only higher plants were taken into account, the percentage of plant biomass located below ground increased with altitude from 21% in the blanket mire to 62% in the *Racomitrium* heath. As for NPP, winter soil conditions were most closely related to the size of the AGB C pool (Table 3). In this case AGB C was positively related to mean winter soil temperatures, the model fit was improved further by including mean bryophyte cover which was also positively related to AGB ( $AGB = 0.46 * \text{winter temp} + 0.004 * \text{bryophyte cover} - 0.17$ ;  $R^2 = 0.99$ ;  $F_{2,4} = 1010.59$ ;  $P < 0.001$ ).



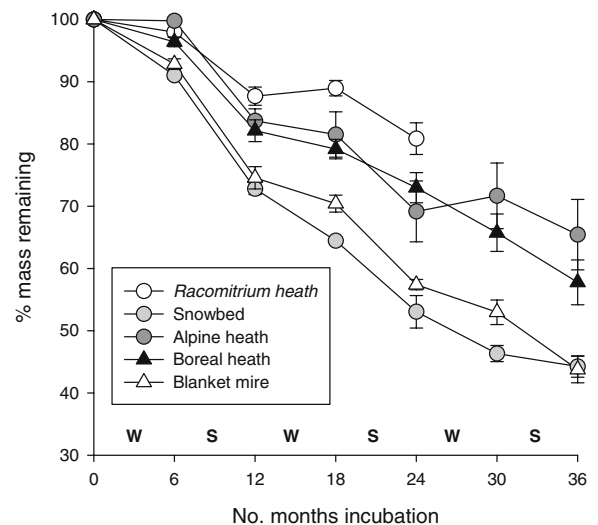
**Fig. 2** Carbon pools in five habitats along a boreal-alpine toposequence; a) vegetation biomass and litter C pools b) total ecosystem C pools (vegetation + soils)

AGB was also significantly correlated with NPP ( $AGB = 0.0085 * NPP - 0.024$ ;  $R^2 = 0.80$ ;  $F_{1,4} = 16.66$ ;  $P = 0.027$ ).

### Decomposition

Analysis of the initial chemical composition of litter from the 5 habitats revealed significant differences in %N ( $F_{4,24} = 76.31$ ;  $P < 0.001$ ), %C ( $F_{4,24} = 71.48$ ;  $P < 0.001$ ) and C:N ( $F_{4,24} = 48.25$ ;  $P < 0.001$ ) but no significant difference in N:P. Litter C:N increased in the order: alpine heath < snowbed < blanket mire < boreal heath < *Racomitrium* heath, while litter N content decreased in the same order (Table 2). When correlated against the cover of the main plant groups in each habitat, litter C:N was significantly positively related to total bryophyte and lichen cover ( $R^2 = 0.85$ ;  $F_{1,4} = 23.62$ ;  $P = 0.017$ ).

Decomposition of the surface-placed litter was fastest in the blanket mire and snowbed habitats and slowest in the *Racomitrium* heath, with intermediate rates in alpine and boreal heath (Fig. 3). Analysis of mass loss at each time point showed significant differences between habitats ( $F_{4,49} = 7.11-28.13$ ;  $P < 0.001$ ) for every time point from 6 months onwards with their ranking being consistent through time.



**Fig. 3** Percentage litter mass remaining over 3 years of incubation in five habitats along a boreal-alpine toposequence. Error bars represent standard error of the mean. The letters S and W indicate summer (May–October) and winter (November to April) periods respectively

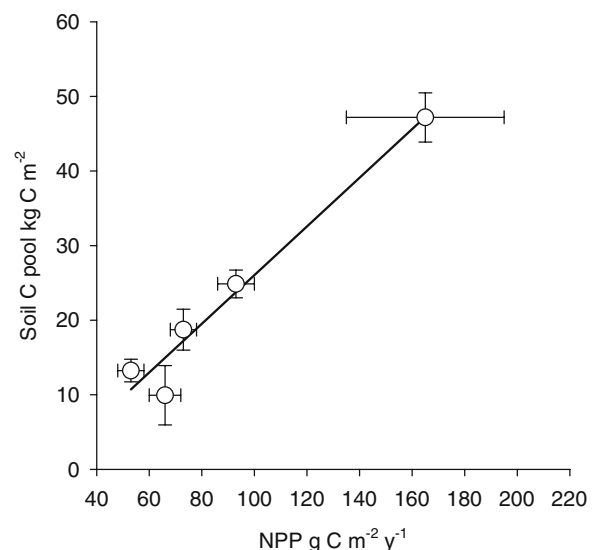
After 36 months incubation, less than 50% of initial litter mass remained in the snowbed and blanket mire, while 60–65% remained in the alpine and boreal heath. In the *Racomitrium* heath, measurements of mass loss ceased after 24 months due to in-growth of moss shoots into the litter bags, but at this point >80% of the initial litter mass remained. The annual mass loss rate ( $k$ ) was determined for each habitat by fitting an exponential curve to the proportional mass remaining data with the origin constrained to 1. Mass loss rates decreased in the order: snowbed > blanket mire > alpine heath = boreal heath > *Racomitrium* heath (Table 2). The influence of initial litter chemistry and environmental variables (soil temperature and moisture, GSL, GDD, FH, Altitude) on between habitat variability in decomposition rates was investigated by correlating these against the  $k$  values for each habitat (Table 3). Mean site decomposition rate was best explained by a combination of initial litter C:N and mean annual soil moisture ( $k=0.003*\text{mean annual moisture} - 0.004*\text{C:N}+0.279$ ;  $R^2=0.99$ ;  $F_{2,4}=660.38$ ;  $P<0.001$ ). There was no significant relationship between temperature and decomposition rate at the between habitat level.

Variability in mass loss between seasons and over time was investigated by determining mean litter mass loss in each habitat over each 6-month period and was examined in relation to mean soil temperature and moisture for the period, litter C:N, N:P and %N at the start of each period and duration of incubation (to account for exponential decay). Across all five habitats and all incubation periods, soil temperature was the only single predictor significantly related to mass loss and was positively correlated ( $R^2=0.45$ ;  $F_{1,28}=24.33$ ;  $P<0.001$ ). Addition of incubation duration improved the model fit ( $R^2=0.59$ ;  $F_{2,28}=20.78$ ;  $P<0.001$ ) and was negatively related to mass loss. At most sites a clear difference could be seen between summer and winter periods (Fig. 3) with the majority of mass loss taking place over the warmer summer months (May – October). Within individual habitats, a significant relationship between mass loss and soil temperature was seen in *Racomitrium* heath ( $R^2=0.87$ ;  $F_{1,3}=21.51$ ;  $P=0.043$ ), alpine heath ( $R^2=0.70$ ;  $F_{1,5}=12.66$ ;  $P=0.024$ ) and blanket mire ( $R^2=0.62$ ;  $F_{1,5}=9.20$ ;  $P=0.039$ ). There was no significant relationship between mass loss and soil temperature in the snowbed or boreal heath.

## Ecosystem C pools

The total ecosystem C pool was large in all five habitats, especially in the blanket mire which held a total pool of  $49.8 \text{ kg C m}^{-2}$  (Fig. 2b). In the other four habitats, C pool sizes ranged from  $11.5\text{--}26.1 \text{ kg C m}^{-2}$  with the largest pool in the snowbed and the smallest in the *Racomitrium* heath. Ecosystem C pools were dominated by soil C which represented 87–95% of the total pool in all habitats (Table 2; Fig. 2b). AGB and BGB represented a small proportion of the total pool and were of similar magnitude to the litter pool in most habitats (Table 2; Fig. 2).

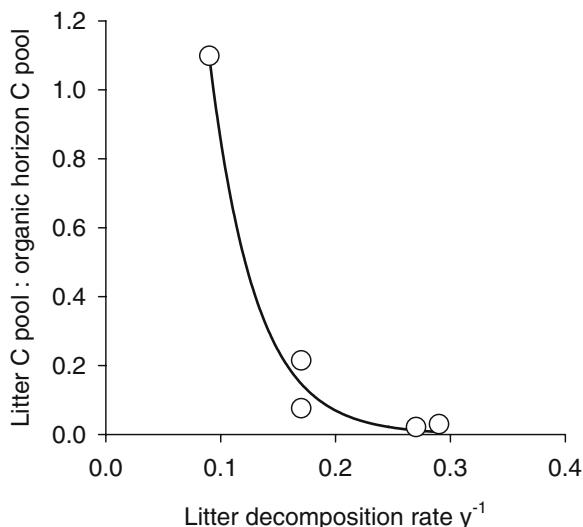
Total soil C pool size represents the integration of conditions of C accumulation or depletion over the very long term, while measurements of climatic conditions and ecosystem properties represent a snapshot of contemporary conditions. Notwithstanding this, we correlated total soil C pool and total ecosystem C pool with soil temperature and moisture, GDD, GSL, FH, altitude, community composition, NPP and decomposition rates in order to investigate how C storage related to variation in conditions across the range of habitats (Table 3). Total soil C pool was strongly positively correlated with NPP (Fig. 4) and



**Fig. 4** Mean total soil C pool size in five boreal/alpine habitats versus mean above ground net primary productivity (NPP). Error bars show standard error of the mean. The line indicates a significant linear relationship (mean soil C pool =  $0.326 \text{ NPP} - 6.55$ ;  $R^2=0.95$ ;  $F_{1,4}=71.65$ ;  $P=0.003$ )

when AGB was included, the total ecosystem C pool was also strongly correlated with NPP (Table 3; Total ecosystem C pool =  $0.339 \text{ NPP} - 6.15$ ;  $R^2=0.95$ ;  $F_{1,4}=85.82$ ;  $P=0.003$ ) being equivalent to approximately 280 years of current NPP in all habitats except *Racomitrium* heath which held only 170 years of NPP. Total pool size was also negatively correlated with FH ( $R^2=0.83$ ;  $F_{1,4}=20.03$ ;  $P=0.021$ ) and positively correlated with mean winter soil temperature ( $R^2=0.71$ ;  $F_{1,4}=10.98$ ;  $P=0.045$ ) but there was no significant influence of the other environmental variables, of decomposition rate or of community composition.

The relationships between community composition, productivity, decomposition rate, temperature and moisture variables and growing season length and the relative size of C pools in biomass, litter and organic and mineral soil horizons were also explored. The amount of C stored in the litter layer per unit AGB was primarily related to community composition, declining as shrub cover increased ( $R^2=0.75$ ;  $F_{1,4}=12.73$ ;  $P=0.038$ ). The size of the litter pool relative to that in the soil organic horizon was, however, strongly influenced by decomposition rate and declined rapidly as decomposition rate increased (Fig. 5). The amount of C storage in the soil organic vs mineral horizon was not affected by community



**Fig. 5** Ratio of carbon stored in litter: soil organic horizons versus litter decay constant (proportion lost per year). Note that ratio and decay constant values are single mean values per habitat type so there is no estimation of within-habitat error. The line indicates a significant exponential relationship ( $y = 10.49 e^{-25x}$ ;  $R^2=0.98$ ;  $F_{1,4}=244.06$ ;  $P<0.001$ )

composition or litter decomposition rate but increased with NPP ( $R^2=0.89$ ;  $F_{1,4}=34.10$ ;  $P=0.010$ ), such that habitats with high NPP (and hence large total ecosystem C pool) tended to have a high proportion of C stored in the organic horizons, while unproductive habitats tended to have more C in the mineral horizons (Table 2).

## Discussion

### Ecosystem C pool sizes

As is typically the case in non-forested ecosystems (De Deyn et al. 2008; King et al. 1997) the ecosystem C pools in the habitats investigated in this study were dominated by the soil C store. Estimates of global average soil C pools in arctic/alpine tundra, cold deserts, moss dominated bogs and sclerophyllous shrublands range from 10–25  $\text{kg C m}^{-2}$  (Amundson 2001; De Deyn et al. 2008; King et al. 1997). The range of soil C pools observed in this study was considerably greater, from 9.9–47.2  $\text{kg C m}^{-2}$ , indicating that soil C pools in these habitats may have been significantly underestimated. Despite the low stature of the boreal and alpine vegetation types considered here and thus the relatively small additional contribution of AGB to the total C store, the total ecosystem C pool in these habitats was at the high end of the range calculated for major vegetation types world wide (King et al. 1997) emphasising the importance of C stocks held within oceanic alpine landscapes.

Estimates of soil C pools in this study were similar to those from recent studies in more continental alpine regions such as the European Alps and Pyrenees which give values of 5–38  $\text{kg C m}^{-2}$  for habitats above the treeline (Djukic et al. 2010; Garcia-Pausas et al. 2007; Leifeld et al. 2009). Many of these studies are focussed on grassland habitats however, while in oceanic alpine zones shrub- and moss-dominated habitats with highly organic soils are much more prevalent; in the UK, *Nardus*-dominated snowbeds, *Racomitrium* heath and alpine *Calluna* heath represent 25%, 24% and 17% of total alpine vegetation cover respectively (Thompson and Brown 1992). One previous study of alpine soils from the UK (Grieve 2000) reported values of 0.7–12.8  $\text{kg C m}^{-2}$  for the soil C store in a similar range of alpine habitats—this

is considerably lower than the values in our study, but may reflect the higher altitudes at which they sampled (970–1300 m asl vs. 620–908 m asl in this study). Studies using single vegetation types such as grassland have shown that soil C storage tends to decline as a community reaches its upper altitudinal limit (Djukic et al. 2010; Garcia-Pausas et al. 2007). Clearly, extensive sampling across the range of each habitat will be required to develop a full understanding of variability in C stocks along altitudinal and environmental gradients and to allow more accurate calculation of the total pools held within any particular landscape.

#### Primary production and biomass C pools

The NPP values measured in this study fell within the range cited for alpine habitats worldwide—generally 100–400 g m<sup>-2</sup> y<sup>-1</sup> for closed alpine vegetation (Carnioli et al. 2009; Körner 1999). In contrast to our first hypothesis, NPP did not decline with altitude along the topographic gradient. While there was a significant drop in NPP between blanket mire and the other habitats, there was no consistent change in NPP from the boreal heath at 640 m to the ridge top at 908 m; rather, the altitudinal gradient was dominated by between-community variability. The importance of topographic position for determining NPP has previously been shown in alpine vegetation (Bowman and Fisk 2001) and related to gradients in moisture and nutrient availability (Fisk et al. 1998). While our analysis of drivers of between habitat variability is limited in scope, mean number of frost hours was negatively correlated with NPP, suggesting that winter cold restricts productivity, rather than summer warmth or growing season length as represented by GDD and GSL using a 5°C baseline. However, this did not account for the locally high productivity in the (wet) snowbed and low productivity in the (dry) alpine heath which suggest a potential additional role of topographic moisture gradients; a more extensive study would be required to confirm this hypothesis.

AGB varied greatly between habitats within the alpine zone as seen in previous studies (e.g. Carnioli et al. 2009) but was within the range recorded for these habitats (Körner 1999). Notably the proportion of plant biomass below ground was low in our study compared with others (e.g. Körner 1999; Bowman and Fisk 2001; Carnioli et al. 2009; Nagy and

Grabherr 2009) especially in the lower altitude habitats, although it did increase with altitude as previously reported (Hitz et al. 2001). In part this was due to the high biomass of bryophytes and lichens which is a particular feature of oceanic alpine habitats, but it likely also reflects the difficulty of separating fine roots from organic soils and some root biomass may have been accounted for within the soil C pool.

#### Decomposition

Litter decomposition rates were slow in all habitats with only the faster rates at the snowbed and blanket mire being comparable with rates previously reported from alpine tundra in the USA (O’Lear and Seastedt 1994) and European alps (Baptist et al. 2010). The generally slow rates of decomposition reflect the prevalence of ericaceous shrubs, mosses (especially *Sphagnum* and *Racomitrium*) and lichens which are known to produce recalcitrant litter with high C:N and low quality C which degrade extremely slowly (Aerts 2006; Hobbie 1996; Lang et al. 2009). As in previous studies of decomposition rates along altitudinal gradients (Murphy et al. 1998; Withington and Sanford 2007) we did not find a linear decrease in decomposition with altitude, but found that decomposition varied between habitats, with two adjacent habitats, *Racomitrium* heath and snowbed, having the slowest and fastest rates of decomposition respectively. Indicative analysis of links between litter quality, environmental drivers and decomposition rates at the between habitat level suggested that litter quality was an important control on decomposition, with initial litter C:N being negatively related to mass loss during the 3 year incubation. However, contrary to our initial hypothesis that moisture would be less limiting to decomposition than temperature in the cool, wet oceanic alpine environment (rainfall >1000 mm y<sup>-1</sup>) soil moisture did appear to contribute to the differences in decomposition between habitats, while soil temperature had no significant effect. Waterlogged habitats such as mires are often associated with slow decomposition but in this system we show that, for litter present at the surface, decomposition was fastest in the wettest habitats. While at first glance this may seem surprising, similar results have been found in alpine environments in the USA where decomposition rates have been shown to peak at intermediate moisture values (Bryant et al. 1998; O’Lear and Seastedt 1994; Withington and

Sanford 2007). Seastedt et al. (2001) suggested that the number of communities where decomposition of surface placed litter declines in response to excess moisture may be extremely limited, as decomposition rates even in wet communities can still be very high provided that prolonged periods of anaerobic conditions do not occur. This was also the case in our study and emphasises that surface drying may be a major constraint on decomposition even in oceanic alpine environments.

While temperature did not have a significant effect on the between habitat variability in decomposition, it was the major driver of seasonal variability. Temperature-driven seasonal differences in mass loss were seen in three of the five habitats, with reduced mass loss over the winter period. The slower decomposition during winter suggests a potentially positive response to climate warming scenarios, however, studies in continental alpine systems have suggested that mass loss of litter during winter is greatest where snow pack protects soils from winter freezing but does not limit summer soil temperatures (Baptist et al. 2010; O’Lear and Seastedt 1994). A positive effect of snow cover was seen in this study where alpine and *Racomitrium* heaths, occupying exposed snow-free locations, showed negligible mass loss during winter, while in the adjacent snowbed which generally had some snow cover, litter mass loss continued through the winter period. In this system, warmer winter temperatures might be expected to increase annual mass loss rates in the exposed habitats which are currently without snow cover, while loss of snowpack could lead to a slowing of decomposition in snowbed habitats. This is in contrast to continental alpine habitats where the majority of habitats have winter snow cover and a warming-induced thinning of the snow pack could lead to increased soil freezing and a reduction in overall rates of decomposition in most habitats (Baptist et al. 2010). Gavazov (2010) in a review of studies in (mainly continental) alpine habitats suggested that reduced soil moisture, loss of insulating snowpack and the expansion of shrubs could offset the effects of warming on decomposition, leading to internal buffering of carbon pools against the effects of climate change. In this oceanic-alpine system, most habitats are already snow-free for much of the winter and dominated by ericaceous shrubs or equally recalcitrant bryophytes, suggesting fewer potential offsets to the effects of warmer temperatures. Future changes in soil moisture regimes thus seem

likely to be important for determining overall decomposition response to increased temperature, both through direct effects and via indirect effects on species’ distributions.

Inter-relationships between production, decomposition and C pool sizes

The lack of linear trends in productivity and decomposition along the toposequence resulted in total ecosystem C pools varying on a habitat-specific basis, supporting our third hypothesis. Rather than representing a balance between contemporary NPP and decomposition rates however, we found that total C pool size was closely related to NPP with little influence of decomposition rate. In part this may reflect the fact that decomposition rates were very low in all of the habitats compared to those seen in other biomes (Harmon et al. 2009) resulting in rates of C accumulation and hence total C pool size being influenced primarily by the rate of C input from NPP. However, this finding could also suggest that rates of C-loss are in fact similar across all habitats (assuming all habitats have been accumulating C for the same period of time) contrary to the measured differences in surface litter decomposition rate. One reason for this apparent discrepancy may be that in some habitats there could be multiple litter pools which experience differing environmental conditions and have different decay rates. For example in the two wettest habitats, snowbed and blanket mire, surface placed litter decomposed very quickly but soil C pools were large. In these habitats higher plant leaf litter is found at the ground surface and its decomposition rate would be accurately represented by the surface placed litter bags, however, bryophyte litter (especially of carpet forming genera such as *Sphagnum*) is produced at the base of the bryophyte mat and may experience waterlogged, anaerobic conditions due to the high water table. Coupled with the typically recalcitrant nature of bryophyte litter (Lang et al. 2009) this deeper litter pool could be expected to decompose much more slowly than the surface pool and make a larger contribution to long term C sequestration. Depending on their relative size, the combination of these two pools could result in similar overall C-loss rates across habitats. It must also be considered that the soil C pool, which dominates the total ecosystem C pool, represents the outcome of net



carbon accumulation or depletion over the long term. Climatic conditions and hence productivity and decomposition rates will almost certainly have varied over the period during which the soil C pool has developed and this must be borne in mind when comparing the accumulated C pool with contemporary measurements of ecosystem properties. For example, in the case of *Racomitrium* heath, decomposition rates were half those in the other habitats, yet total C pool size was only 170 times NPP compared with 280 times NPP in other habitats, suggesting a faster C-loss rate than that currently measured in litter decomposition, or a shorter period of accumulation. Exposed mountain summit habitats such as this one are strongly influenced by the wind which may redistribute litter to more sheltered habitats and cause periodic erosion of the moss carpet and underlying soil layers. Wind and water have previously been suggested as major agents of nutrient redistribution within alpine habitats (Seastedt et al. 2004) and such exports could partly account for the lower than expected total C pool. An alternative scenario is that this mountain summit location may have been colonised by the *Racomitrium* heath community more recently than is the case for lower altitude vegetation types, resulting in a shorter period of C accumulation. The vegetation zone immediately above *Racomitrium* heath is typically occupied by sparse fell-field communities and boulder fields; such habitats might be expected to have extremely low rates of C accumulation and relatively recent replacement of such a community by *Racomitrium* heath could explain the lower than expected total C pool size.

## Conclusion

Our study has shown that oceanic alpine habitats can contain significant stores of C and are among the most C-dense ecosystems on a global scale (King et al. 1997). Litter decomposition rates were slow in all habitats, reflecting the prevalence of ericaceous dwarf shrubs, bryophytes and lichens and their low quality litter (Lang et al. 2009). Since decomposition (and hence output from the ecosystem C pool) is slow, variability in total C pool between habitats closely reflects inputs from NPP. Neither NPP nor decomposition showed any consistent variation with altitude along the toposequence, but rather reflected the importance of spatial variability in environmental conditions within

the alpine zone which has also been highlighted by other workers (Bowman and Fisk 2001; Seastedt et al. 2001). Despite high rainfall in this oceanic ecosystem, both rainfall and temperature appeared to significantly influence aspects of C input to and output from the total ecosystem C pool emphasising the potential for predicted changes in climate to influence C storage in oceanic alpine landscapes.

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