Formation of forest gaps accelerates C, N and P release from foliar litter during 4 years of decomposition in an alpine forest

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Formation of forest gaps accelerates C, N and P release from foliar litter during 4 years of decomposition in an alpine forest

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Abstract Relative to areas under canopy, the soils in forest gaps receive more irradiance and rainfall (snowfall); this change in microclimate induced by forest gaps may influence the release of carbon (C) and nutrients during litter decomposition. However, great uncertainty remains about the effects of forest gaps on litter decomposition. In this study, we incubated foliar litters from six tree and shrub species in forest gaps and canopy plots and measured the release of C, nitrogen (N) and phosphorus (P) in different snow cover periods in an alpine forest from 2012 to 2016. We found that N was retained by 24–46% but that P was immediately released during an early stage of decomposition. However, forest gaps decreased litter N retention, resulting in more N and P being released from decomposing litters for certain species (i.e., larch, birch and willow litters). Moreover, the release of C and nutrients during litter decomposition stimulated by forest gaps was primarily driven by warmer soil temperature in this high-altitude forest. We conclude that gap formation during forest regeneration may accelerate C turnover and nutrient cycling and that this stimulation might be regulated by the litter species in this seasonally snow-covered forest.

Keywords Alpine forest · Forest gap · Litter decomposition · Nitrogen retention · Phosphorus release

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Introduction

Forest gaps lead to increasing irradiance and rainfall (or snowfall), resulting in altered soil temperature and moisture compared with areas under canopy (Gray et al. 2002; Ritter et al. 2005). Changes in environmental conditions induced by gap formation can alter litter chemistry and microbial activity and further affect nutrient release during litter decomposition (Zhang and Liang 1995). The faster decomposition of plant litter resulting from higher temperature and moisture may also stimulate soil nitrogen (N) mineralization and inorganic N leaching (Denslow et al. 1998; Ritter 2005; Scharenbroch and Bockheim 2007), thus increasing the N availability for soil microorganisms and potentially reducing the critical C/N ratio during the net release of N from decomposing litter (Manzoni et al. 2010).

Previous studies have found that the effect of forest gaps on decomposition rates begins after 60 days of decomposition (Zhang and Zak 1995) and lasts for at least 4–5 years (Prescott et al. 2003; Sariyildiz 2008). The size of forest gaps necessary to change litter decomposition is less clear, but litter mass losses have been reported to be altered in gaps ranging from as small as 3 m (Ritter and Bjørnlund 2005) to as large > 30 m in diameter (Zhang and Zak 1995). However, more recent experiments that assessed the effect of forest gaps on carbon (C) and nutrient release during litter decomposition yielded inconsistent results in different forests, with the rates in forest gaps reported to be faster, slower or the same as those under canopy. For instance, some studies have shown that forest gaps increased the decomposition rate of European beech (*Fagus sylvatica*) litter (Bauhus et al. 2004; Ritter 2005; Lin et al. 2015), whereas the mass losses of beech litter were also observed to be lower in forest gaps in other forests (Ritter and Bjørnlund 2005; Sariyildiz 2008). Moreover, forest gaps have been found to decrease the nitrogen (N) and phosphorus (P) release by litters in warm tropical and subtropical forests (Zhang and Liang 1995; González et al. 2014).

The uncertainty of the gap effect could be attributed to the site environment. Prescott et al. (2000) suggested that in cold biomes, the warmer soil temperatures due to canopy openings may stimulate litter mass loss, whereas in warm forests, canopy openings may decrease decomposition because of the drier soils in forest gaps. Our previous studies conducted in an alpine forest on the eastern Tibetan Plateau found that more snow accumulated in forest gaps in winter, resulting in higher soil temperature and microbial biomass relative to the areas under canopy (Ni et al. 2015; He et al. 2016). Meanwhile, the greater leaching of snowmelt water during early spring and more rainfall reaching the soil surface during the growing season may also contribute to the release of C and nutrients from decomposing litter.

The objective of this study was to assess the potential influence of gap formation on biogeochemistry during litter decomposition in this alpine forest. We used litterbags to measure the mass loss, proximate analysis fractions (Li et al. 2016), accumulation of humic substances (Ni et al. 2015) and release of 15 elements (He et al. 2015) in six predominantly foliar litters in this area beginning in 2012. In this study, we presented the C, N and P releases from the six foliar litters during 4 years of decomposition and hypothesized that the C and nutrient releases were greater in forest gaps than in areas under canopy in this alpine forest.

Materials and methods

Experimental site

This study was conducted at the Long-term Research Station of Alpine Forest Ecosystems (31°14′N, 102°53′E and 3579–3582 m a.s.l.), which is located in a 130-year-old fir (*Abies faxoniana*) alpine forest on the eastern Tibetan Plateau, China. The annual mean temperature and precipitation are 2.7 °C and 850 mm, respectively. Seasonal snowfall begins in late October, and snow melts in April of the following year. The dominant trees are fir, cypress (*Sabina saltuaria*), larch (*Larix mastersiana*) and birch (*Betula albosinensis*). Dwarf willow (*Salix paraplesia*) and azalea (*Rhododendron lapponicum*) are the main shrubs, and there are also some sedges (*Carex* spp.) and mosses at the site. The soils are classified as Cambisols (WRB taxonomy), and the C, N and P contents are presented in Table S1. The annual litter fall is 2380 kg ha^{-1} $year^{-1}$ (Fu et al. 2017). Forest gaps cover 23% of the landscape in this alpine forest (Wu et al. 2013).

Experimental design

In 2012, three oval forest gaps (ca. 20 m × 25 m in size and 500-2000 m apart) with similar gap formation patterns (tree fall) and durations (ca. 20 years) were selected as replicates based on our previous investigations (Wu et al. 2013). There are significant differences in microclimate between the southern and northern edges of the gap center (Troendle 1983; Ritter et al. 2005); thus litter samples were incubated in the center of the forest gaps in this study. All of the gap centers were located in areas with aspects of NW 50°–55° and slopes of < 5°. One closed canopy plot (as control) was established adjacent to each gap center at a distance less than 30 m. Each plot was further divided into six subplots to incubate the six dominant foliar litters (fir, cypress, larch, birch, willow and azalea), which have contrasting chemistries (Table S2).

In the fall of 2012, senesced foliage of the six litters was collected on tarpaulins from > 20 trees or shrubs by shaking their limbs. Green or partly decomposed needles (leaves), twigs and bark were removed, and only new foliar litter was air-dried at room temperature for 2 weeks. Air-dried litter samples (10 ± 0.05 g) were placed in nylon litterbags (20 cm × 25 cm in size with mesh sizes of 1.0 mm on top and 0.5 mm on bottom), and a total of 1758 litterbags (2 litterbags × 6 plots × 2 treatments × 6 litter species × 12 sampling times + 5 litterbags × 6 litter species) were carefully transferred to the corresponding subplots on November 15 and 16, 2012. Litterbags in the same subplots were strung together and were separated by 2–5 cm. After all litterbags were established on the soil surface, five litterbags of each litter species were randomly collected and returned to the laboratory to determine the losses during establishment and the water contents of the air-dried litter samples (8–13%).

Sampling and analyses

Winter snow cover and freeze–thaw cycles modulate some key biogeochemical cycles in the studied alpine forest, including litter decomposition (Wu et al. 2010, 2014); therefore, we sampled at the ends of both winter and the growing season (Ni et al. 2015). The beginning and end of each winter were defined as the time at which the hourly temperature had a 50% probability (continual 12 h per day) of dropping below freezing (0 °C; Table S3; modified from Ladwig et al. 2016). Winters were further divided into three stages (snow formation, snow coverage and snowmelt stages) based on snow dynamics and changes in temperature (Ni et al. 2014). In this study, we sampled four times per year (at the ends of the snow formation, snow coverage and snowmelt stages and at the end of the growing season) from 2012 to 2014 but only twice per year (at the ends of the snowmelt stage and the growing season) from 2014 to 2016. On each sampling date, two litterbags per plot (6 plots for both forest gaps and canopy) for each litter species were randomly collected, carefully placed in separate plastic bags and transported to the laboratory. Snow depth was measured manually in triplicate per plot (n = 18) on each sampling date. The temperature of the litter surface (n = 6) was recorded using data loggers (iButton DS1923-F5, Sunnyvale, CA, USA).

Roots, mosses and soils were carefully removed from litter samples. One sample was oven-dried at 105 °C for 48 h to measure its dry mass and gravimetric water content. Another sample was air-dried and milled, and a subsample was used to determine its C, N and P contents via dichromate oxidation, Kjeldahl digestion (KDN, Top Ltd., Zhejiang, China) and phosphomolybdenum yellow spectrophotometry (TU-1901, Puxi Ltd., Beijing, China), respectively (Lu 1999). A 0.5 g air-dried subsample was oven-dried at 105 °C for 48 h to determine its moisture, and its C, N and P contents were calculated by dry mass.

Data calculation and statistical analyses

The peak N content and critical C/N ratio were defined as the point when the net N loss from litter began (Moore et al. 2006). Nitrogen retention was defined as the remaining N relative to the original level (100%) at the peak N content. A freeze–thaw cycle was defined as a transition above or below 0 °C for at least 3 h and then a transition back (Konestabo et al. 2007), and the frequency of freeze–thaw cycles (time day^{-1}) was defined as the quotient of the number of freeze–thaw cycles and the days during a certain period (snow formation, snow coverage and snowmelt stages and growing season).

We used repeated measures analyses of variance (ANOVA) to examine the effects of litter species and

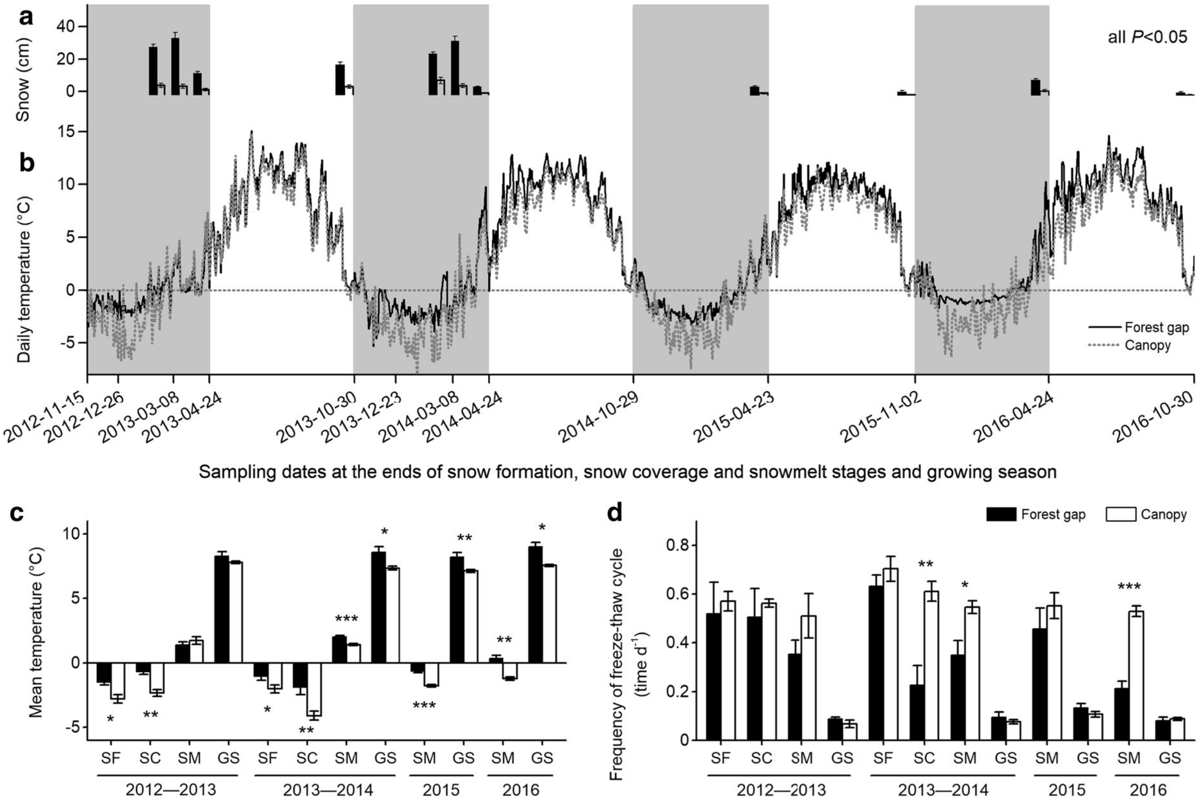

Fig. 1 Snow depths, temperatures and frequency of freeze–thaw cycles. **a** Snow depths (± SE, n = 18) in forest gaps and under canopy on each sampling date. Differences between forest gap and canopy plots are significant ($P < 0.05$) on all sampling dates based on paired t-tests. **b** Daily temperatures (n = 6) on litter surface. Sampling dates are scheduled at the ends of the snow formation, snow coverage and snowmelt stages and at the end of the growing season. Winter times (including snow formation, snow coverage and snowmelt stages) are shaded. **c** Mean temperatures (n = 6) at each stage. Times between two adjacent sampling dates are defined as separate stages. *SF* snow formation stage, *SC* snow coverage stage, *SM* snowmelt stage, *GS* growing season. **d** Frequency of freeze–thaw cycles (n = 6) at each stage. Asterisks denote significant ($P < 0.05$) differences between forest gap and canopy plots on each sampling date based on paired t-tests: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

forest gaps on all variables over time and paired t-tests to compare differences between forest gaps and canopy plots at each sampling date. To assess how N retention determines N release during litter decomposition in this area, the initial N content, initial C/N ratio and peak N content for each litter species were averaged and plotted against the remaining N after 4 years of decomposition for forest gaps and canopy separately. To explore the nutrient release patterns as C was lost, the N and P remaining before, at and after the peak N contents and after 4 years of decomposition were also plotted against the remaining C for forest gaps and canopy separately. Differences between forest gaps and canopy over the study period were determined by analysis of covariance, and relationships between the two variables were assessed by linear regressions for forest gaps and canopy separately. All analyses were performed in MATLAB R2012a (MathWorks Inc., Natick, MA, USA). We also used a structural equation model in AMOS 22.0 (IBM SPSS, Chicago, IL, USA) to examine the direct effect of forest gaps on litter temperature and water content and to compare the relative contributions of temperature and moisture on the C, N and P releases during litter decomposition. The data (n = 864) were resampled 499 times using Monte Carlo methods. The coefficients were estimated using the maximum likelihood method, and the confidence intervals were set at 95%. Differences are significant if $P < 0.05$ for all analyses included in this study.

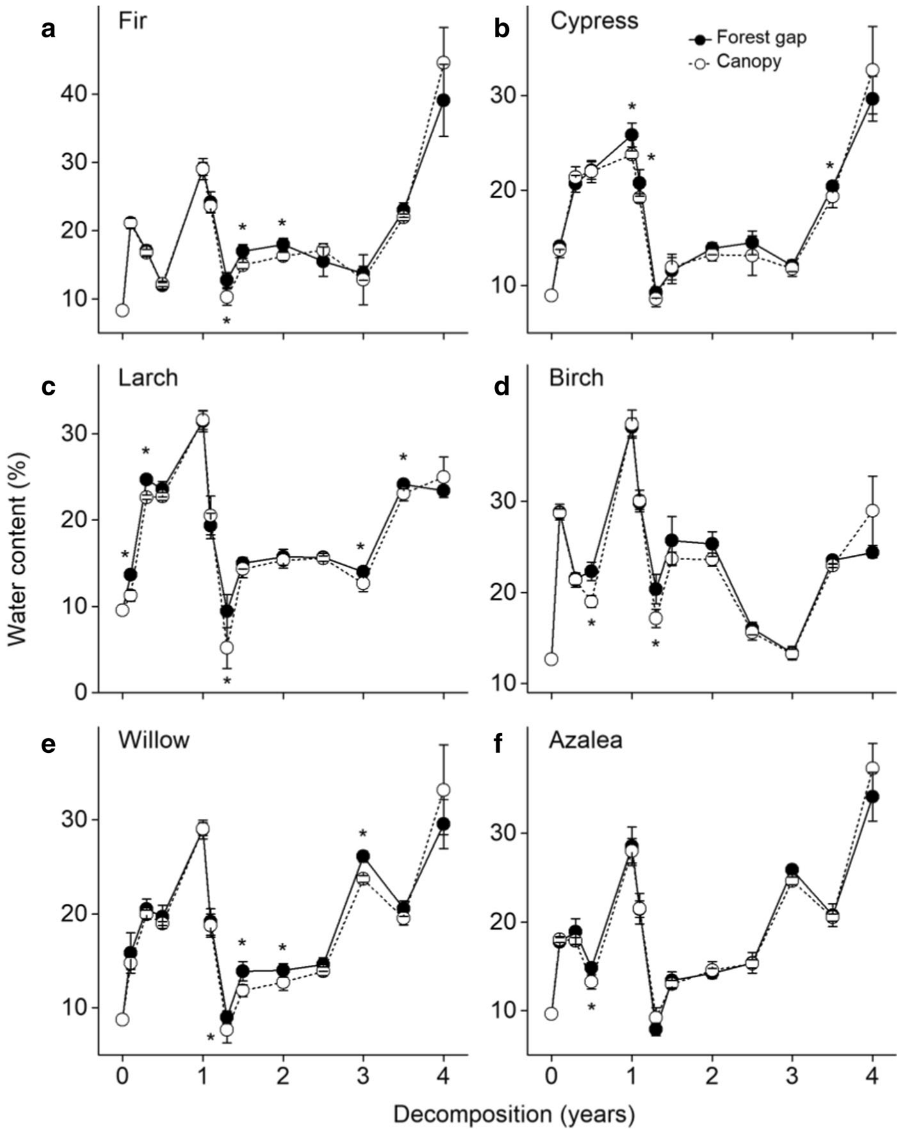

Fig. 2 Water contents (± SE, $n = 6$) in decomposing litters. **a** Fir, **b** cypress, **c** larch, **d** birch, **e** willow, **f** azalea. Asterisks denote significant ($P < 0.05$) differences between forest gap and canopy plots on each sampling date based on paired t-tests

Table 1 Mass remaining in litter after 4 years of decomposition and the percentage of litter mass that decomposed during the winter

Litter	Mass remaining after 4 years (%)			% decomposed in winter		
	Forest gap	Canopy	*P* value	Forest gap	Canopy	*P* value
Fir	47.5 (1.4)	45.5 (2.5)	0.17	66.6 (1.1)	55.6 (4.2)	**0.042**
Cypress	33.7 (1.2)	34.6 (2.1)	0.56	50.9 (3.2)	43.8 (1.8)	0.080
Larch	41.9 (0.3)	44.6 (0.6)	**0.0025**	58.9 (1.6)	46.2 (1.1)	**< 0.001**
Birch	39.3 (1.8)	40.4 (1.4)	0.27	61.7 (1.2)	54.2 (3.0)	0.055
Willow	24.0 (2.4)	26.1 (2.2)	0.40	47.4 (3.9)	47.5 (1.0)	0.99
Azalea	42.8 (2.9)	47.9 (2.9)	**0.0029**	74.1 (2.0)	62.2 (3.7)	0.068

Data are shown as means, with standard errors in parentheses ($n = 6$). Bold *P* values from paired t-tests are significant ($P < 0.05$)

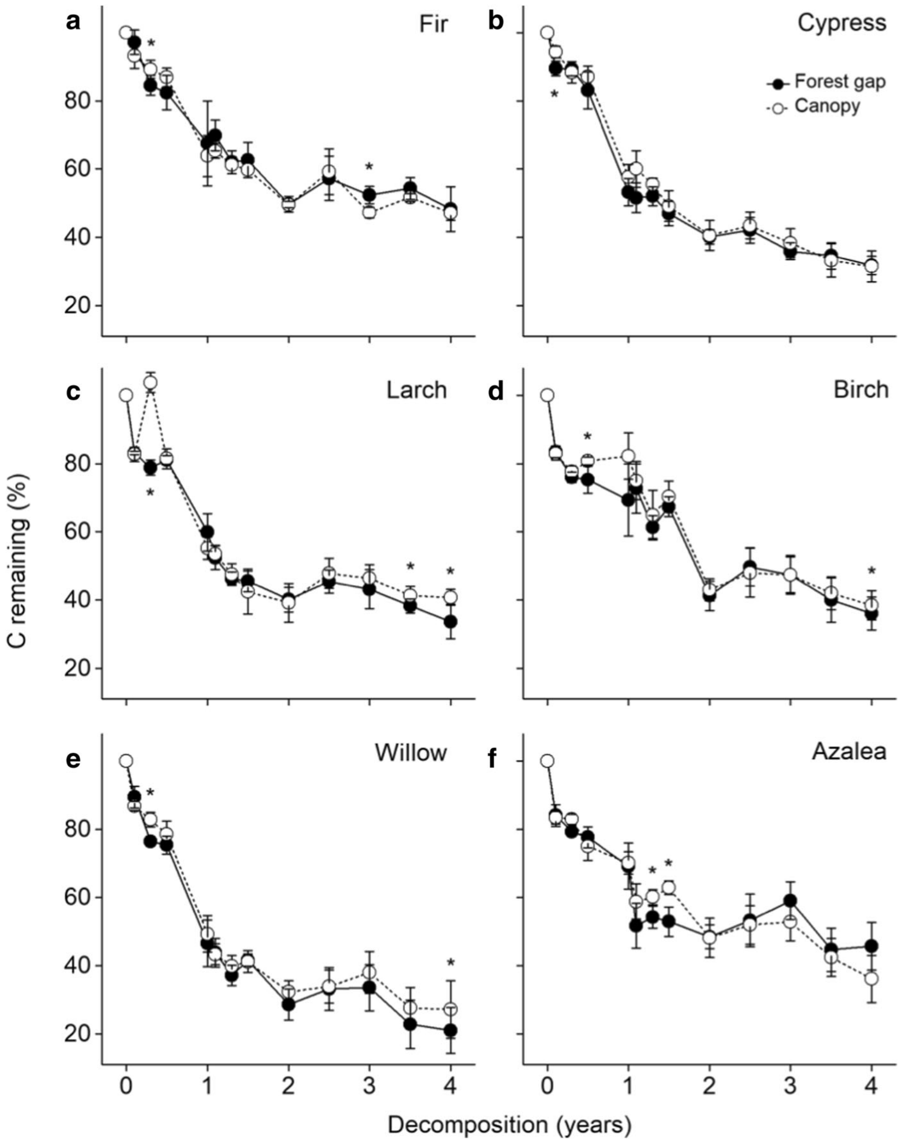

Fig. 3 Carbon (C) remaining (± SE, $n = 6$) in decomposing litters. **a** Fir, **b** cypress, **c** larch, **d** birch, **e** willow, **f** azalea. Asterisks denote significant ($P < 0.05$) differences between forest gap and canopy plots on each sampling date based on paired t-tests

Results

Temperature and water content

Deeper snow was observed in forest gaps than in canopy plots on all sampling dates (all $P < 0.05$; Fig. 1a). Compared with the canopy plots, the forest gaps showed higher temperatures (Fig. 1b, c) but a lower frequency of freeze–thaw cycles (Fig. 1d). The litter water content increased by 129–435% across litter species after 4 years of decomposition, and higher values were observed in forest gaps than in canopy plots (Fig. 2).

Litter mass remaining

After 4 years of decomposition, the remaining masses of fir, cypress, larch, birch, willow and azalea litters were 46, 35, 45, 40, 26 and 48%, respectively, in canopy plots (Table 1). Larch and azalea litters had lower ($P < 0.01$) remaining mass in forest gaps than in canopy plots. In forest gaps, more than 50% of the litter mass (except for willow litter) was lost during the winter, and the percentages of the litter mass that decomposed during winter were higher in forest gaps than in canopy plots for fir ($P = 0.042$) and larch ($P < 0.001$) litters (Table 1).

Table 2 Carbon (C), nitrogen (N) and phosphorus (P) remaining in litter after 4 years of decomposition

Litter	C remaining (%)			N remaining (%)			P remaining (%)		
	Forest gap	Canopy	*P* value	Forest gap	Canopy	*P* value	Forest gap	Canopy	*P* value
Fir	48.3 (2.7)	47.1 (0.9)	0.58	37.5 (2.2)	39.4 (1.4)	0.20	54.7 (7.1)	49.8 (1.9)	0.097
Cypress	31.8 (1.1)	31.5 (1.9)	0.80	28.2 (1.5)	30.2 (2.4)	0.28	38.4 (2.0)	37.6 (3.1)	0.62
Larch	33.7 (2.1)	40.8 (1.0)	**0.0078**	30.6 (0.6)	36.0 (1.3)	**0.0029**	36.3 (0.5)	37.3 (0.6)	0.28
Birch	36.0 (2.0)	38.5 (1.8)	**0.047**	18.8 (0.9)	22.8 (1.1)	**< 0.001**	50.6 (2.5)	77.3 (10.8)	**0.033**
Willow	21.0 (2.7)	27.2 (3.4)	**0.028**	13.0 (1.6)	17.7 (2.0)	**0.0083**	25.0 (2.4)	31.6 (3.2)	0.095
Azalea	45.8 (6.9)	36.1 (6.9)	0.065	42.1 (2.7)	37.8 (3.1)	0.080	72.6 (7.1)	59.8 (2.1)	0.21

Data are shown as means, with standard errors in parentheses ($n = 6$). Bold *P* values from paired t-tests denote significant ($P < 0.05$) differences between forest gap and canopy plots

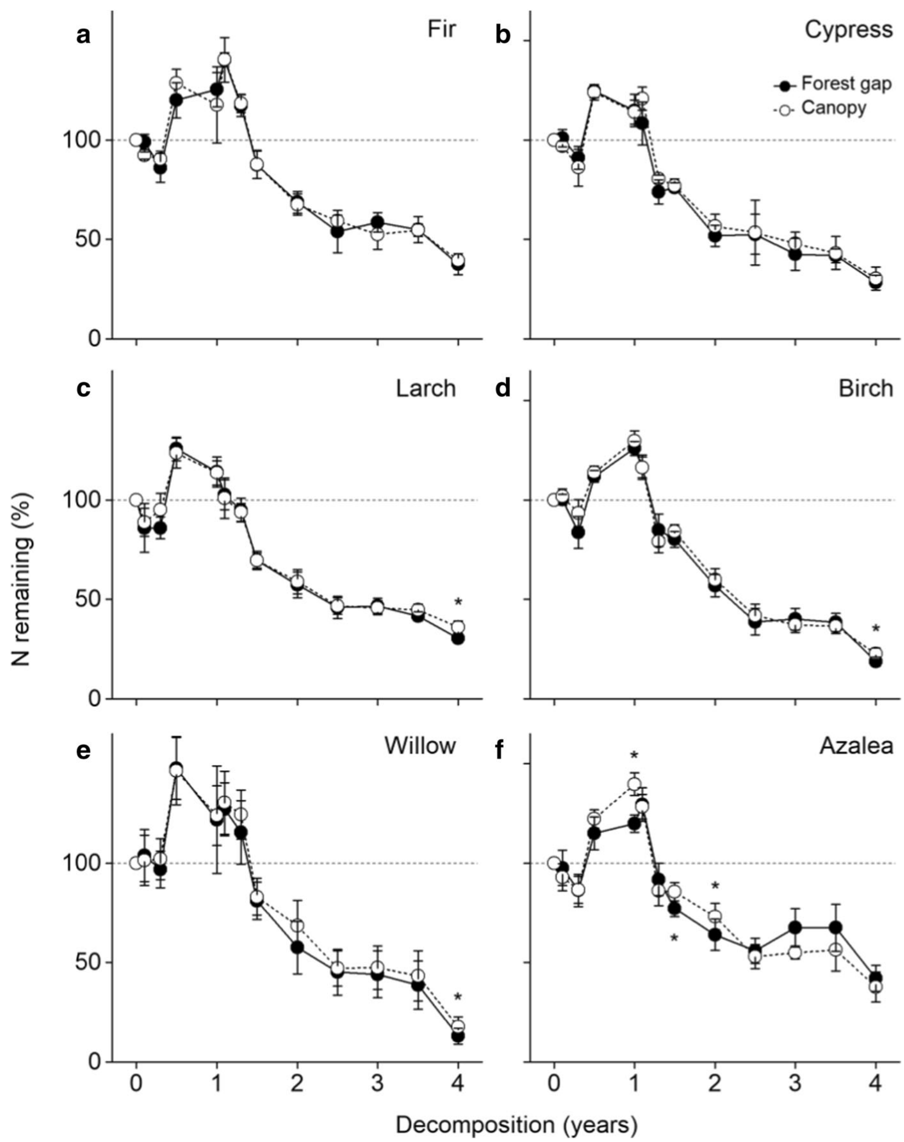

Fig. 4 Nitrogen (N) remaining (± SE, $n = 6$) in decomposing litters. **a** Fir, **b** cypress, **c** larch, **d** birch, **e** willow, **f** azalea. Asterisks denote significant ($P < 0.05$) differences between forest gap and canopy plots on each sampling date based on paired t-tests

Table 3 Carbon (C), nitrogen (N) and phosphorus (P) contents and ratios at the initial stages, during peak N content periods and after 4 years of decomposition

Litter	C content (%)			N content (%)			P content (%)			C/N ratio		
	Initial	Critical	4 years	Initial	Critical	4 years	Initial	Critical	4 years	Initial	Critical	4 years
Fir	50.6^{a}	47.7^{ab}	51.9^{a}	0.88^{c}	1.72^{b}	0.72^{ab}	0.11^{b}	0.12^{ab}	0.13^{ab}	57.8^{b}	27.8^{c}	71.9^{ab}
Cypress	51.6^{a}	50.8^{a}	47.9^{ab}	0.88^{c}	1.26^{c}	0.75^{a}	0.12^{ab}	0.11^{b}	0.14^{ab}	58.8^{b}	40.4^{a}	64.2^{b}
Larch	54.4^{a}	51.0^{a}	46.7^{ab}	0.86^{c}	1.24^{c}	0.66^{b}	0.13^{a}	0.10^{c}	0.11^{b}	63.3^{b}	41.3^{a}	70.7^{ab}
Birch	49.7^{ab}	47.0^{ab}	46.3^{ab}	1.33^{a}	2.12^{a}	0.69^{ab}	0.09^{c}	0.11^{bc}	0.15^{ab}	37.2^{c}	22.1^{d}	67.0^{b}
Willow	45.2^{b}	44.2^{b}	43.0^{b}	1.15^{b}	2.13^{a}	0.69^{ab}	0.11^{b}	0.12^{a}	0.12^{b}	39.7^{c}	20.8^{d}	62.7^{b}
Azalea	50.3^{a}	42.1^{b}	45.6^{ab}	0.67^{d}	1.23^{c}	0.59^{c}	0.11^{bc}	0.10^{c}	0.16^{a}	75.5^{a}	34.1^{b}	78.0^{a}

	C/P ratio			N/P ratio		
	Initial	Critical	4 years	Initial	Critical	4 years
Fir	443^{bc}	400^{b}	407^{a}	7.7^{c}	14.4^{c}	5.7^{a}
Cypress	416^{c}	451^{a}	352^{ab}	7.1^{c}	11.2^{d}	5.5^{a}
Larch	408^{c}	497^{a}	411^{a}	6.5^{c}	12.0^{d}	5.8^{a}
Birch	544^{a}	446^{a}	344^{ab}	14.6^{a}	20.1^{a}	5.1^{a}
Willow	408^{c}	364^{b}	347^{ab}	10.4^{b}	17.5^{b}	5.5^{a}
Azalea	470^{b}	412^{b}	289^{b}	6.2^{c}	12.1^{d}	3.8^{b}

Different superscript letters in the same column denote significant ($P < 0.05$) differences among the six litter species based on one-way ANOVA followed by multiple comparisons

C remaining

Although the C content decreased during the first 2 years but increased during the third year of decomposition (Fig. S1), the remaining C consistently decreased over the four-year period (Fig. 3). At the end of this experiment, the remaining C ranged from 27 to 47% across litter species in canopy plots (Table 2). The remaining C varied significantly between forest gaps and canopy plots ($P < 0.001$; Table S4), and after 4 years of decomposition, larch, birch and willow litters showed lower (all $P < 0.05$) levels of remaining C in forest gaps than in canopy plots (Table 2).

N remaining

The N content increased by 40–104% during the first year of decomposition (Fig. 2), resulting in an increase in the remaining N. Thereafter, the remaining N consistently decreased (Fig. 4). After 4 years of decomposition, the remaining N ranged from 18 to 39% across litter species in canopy plots (Table 2). The remaining N in larch, birch and willow litters were significantly lower (all $P < 0.01$) in forest gaps than in canopy plots after 4 years of decomposition (Table 2).

The peak N content ranged from 1.2 to 2.1% across litter species (Table 3). Compared with canopy plots, forest gaps showed lower peak N contents for fir and birch litters, critical C/N ratios for larch, birch and azalea litters and N retentions for birch and azalea litters (all $P < 0.05$; Fig. 5). Nitrogen release after 4 years of decomposition was significantly ($P < 0.05$) correlated with the initial C/N ratio but not for the initial N content in both forest gaps and canopy plots. However, N release at the end of this experiment was significantly related to the peak N content in only forest gaps ($P = 0.038$) and not in canopy plots ($P = 0.83$; Fig. 6). The relationship between remaining N and C loss was positive ($P > 0.05$) before the peak N content was reached and was negative ($P < 0.001$; Fig. 7) afterward in both forest gaps and canopy plots. However, the remaining N after 4 years of decomposition was significantly related to C loss in only forest gaps ($P = 0.027$) and not in canopy plots ($P = 0.11$; Fig. 7).

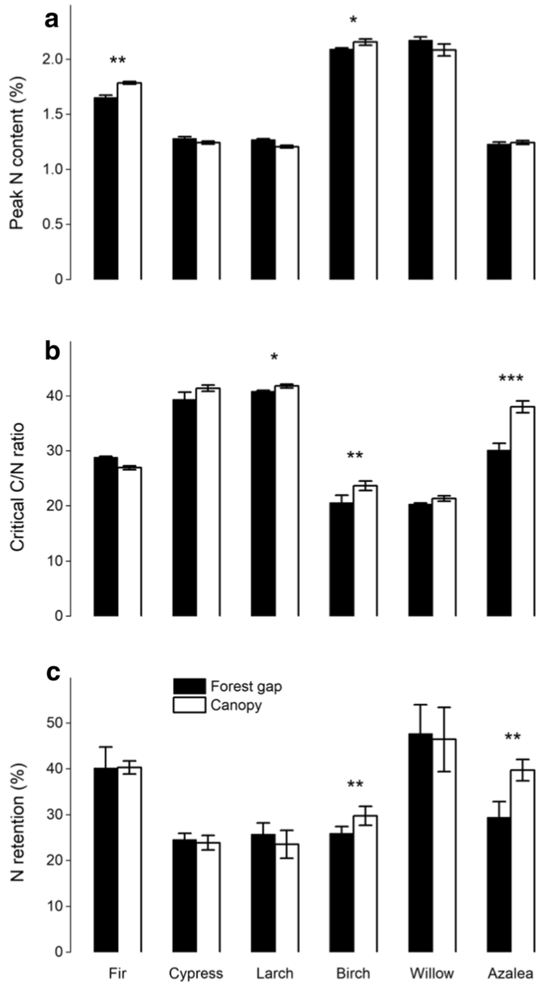

Fig. 5 Critical nitrogen (N) thresholds. **a** Peak N content. **b** Critical C/N ratio. **c** N retention. Values are means (± SE) of the 6 replicates for the six foliar litters in forest gap and canopy plots (n = 12). Asterisks denote significant ($P < 0.05$) differences between forest gap and canopy plots based on paired t-tests: *$P < 0.05$, **$P < 0.01$, $^{***}P < 0.001$

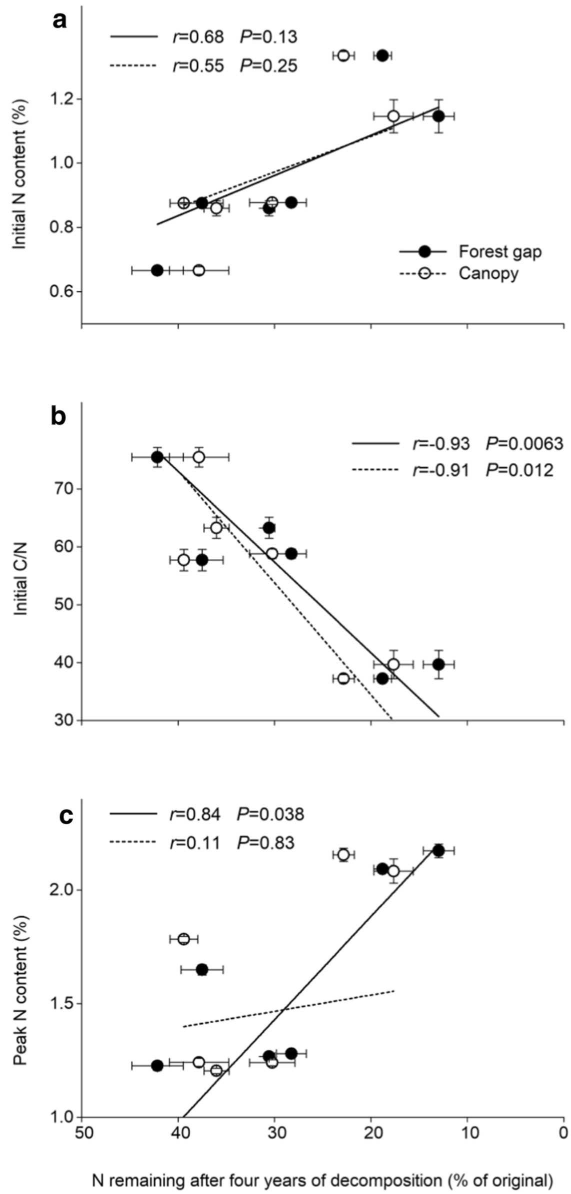

Fig. 6 Remaining nitrogen (N) versus **a** initial N content, **b** initial carbon to nitrogen ratio (C/N) and **c** peak N content. Values are means (± SE, n = 6) for the six foliar litters in forest gaps and under canopy. Pearson's r and P values from linear regressions are shown in each panel. P values between forest gap and canopy plots from analysis of covariance were 0.50, 0.44 and 0.58 for panels (**a**), (**b**) and (**c**) respectively

P remaining

The P content decreased during the first 1.5 years but greatly increased in later periods (Fig. 3), resulting in a rapid decrease in the remaining P during the first year of decomposition for all litter species (Fig. 8). After 4 years of decomposition, the remaining P ranged from 32 to 77% regardless of litter species and was significantly (P = 0.033) lower in forest gaps than in canopy plots for birch litter (Table 2). Remaining P was negatively correlated with C loss before and after ($P < 0.05$) the peak N content was reached in both forest gaps and canopy plots. However, the remaining P after 4 years of decomposition was significantly related to C loss in only forest gaps (P = 0.019) and not in canopy plots (P = 0.46; Fig. 9).

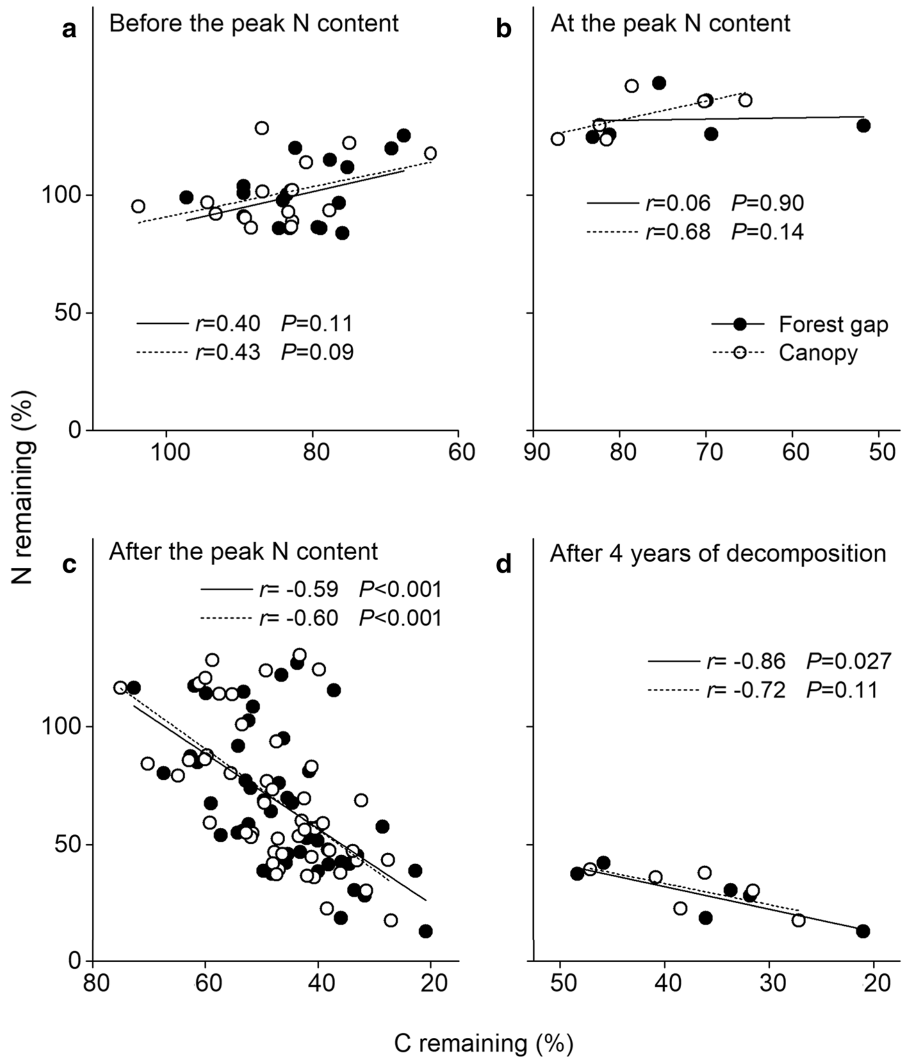

Fig. 7 Remaining carbon (C) versus remaining nitrogen (N). **a** Before the peak N content ($n = 33$). **b** At the peak N content ($n = 12$). **c** After the peak N content ($n = 99$). **d** After 4 years of decomposition ($n = 12$). Values are means ($\pm$ SE, $n = 6$) for the six foliar litters in forest gaps and under canopy. Pearson's r and P values from linear regressions are shown in each panel. P values between forest gap and canopy plots from analysis of covariance were 0.22, 0.30, 0.66 and 0.79 for panels (**a**), (**b**), (**c**) and (**d**) respectively

Factors influencing remaining C, N and P

The results of the structural equation model showed that formation of forest gaps significantly increased the soil temperature but not the water content in decomposing litter (Fig. 10). Soil temperature and the litter water content had negative and positive effects, respectively, on the remaining C, N and P. Compared with litter water content, the effects of soil temperature were greater than those of litter water content.

C, N and P stoichiometry

The initial C/N ratios ranged from 37 to 76 across litter species (Table 3) and decreased during the first year of decomposition. However, these values increased greatly beginning in the second year and ranged from 63 to 78 after 4 years of decomposition (Fig. S4). The critical C/N ratio was 21–41 (Fig. 5). At the end of the experiment, no significant difference in the C/N ratio was observed between forest gaps and canopy plots for all litter species (all $P > 0.05$).

The C/P ratio greatly decreased during the second year of decomposition but increased over the following 2 years (except for azalea litter), ranging from 289 to 411 at the end of the experiment (Fig. 5). The N/P ratio increased greatly during the first year but declined later and ranged from 3.8 to 5.8 after 4 years of decomposition (Fig. 6). Forest gaps were significantly different from canopy plots in terms of both the

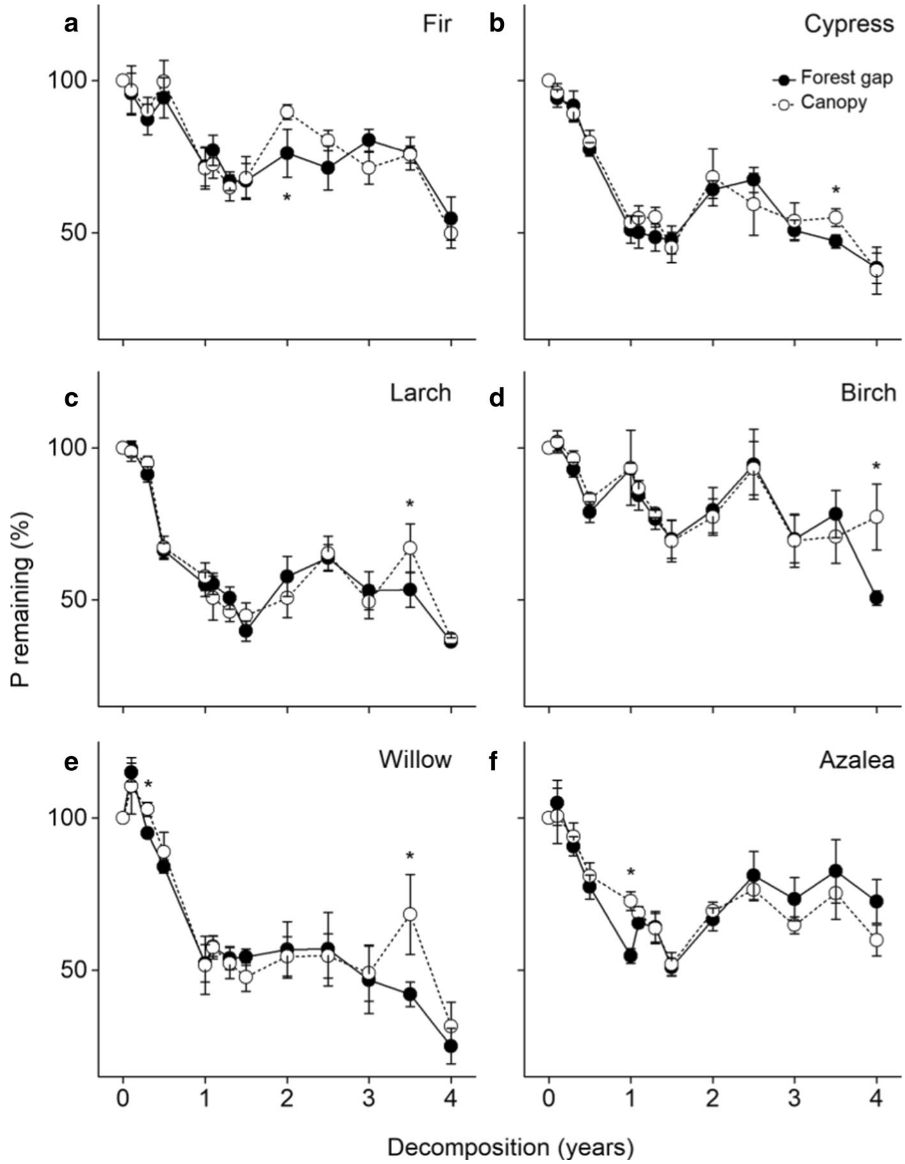

Fig. 8 Phosphorus (P) remaining (± SE, $n = 6$) in decomposing litters. **a** Fir, **b** cypress, **c** larch, **d** birch, **e** willow, **f** azalea. Asterisks denote significant ($P < 0.05$) differences between forest gaps and canopy plots at each sampling date based on paired t-tests

C/P and N/P ratios (both $P < 0.05$; Table S4). After 4 years of decomposition, forest gaps showed a lower C/P ratio in larch litter and lower N/P ratios in fir and larch litters compared with canopy plots.

Discussion

In this study, we found that N was retained, with net N release occurring for C/N ratios of 21–41, but P was immediately released at the beginning of the experiment for all litter species. As hypothesized, formation of forest gaps showed a tendency to stimulate the release of C, N and P from litters during 4 years of decomposition in this high-altitude forest. Two main factors may explain the stimulation of forest gaps in this area: decreased N retention and increased soil temperature.

Release or retention of N and P in decomposing litter largely depends on their initial contents, which determine when the critical C/N or N/P thresholds are reached (Manzoni et al. 2010). Long-term observations have found that litter with a high initial N content retains less N or may even experience net N release

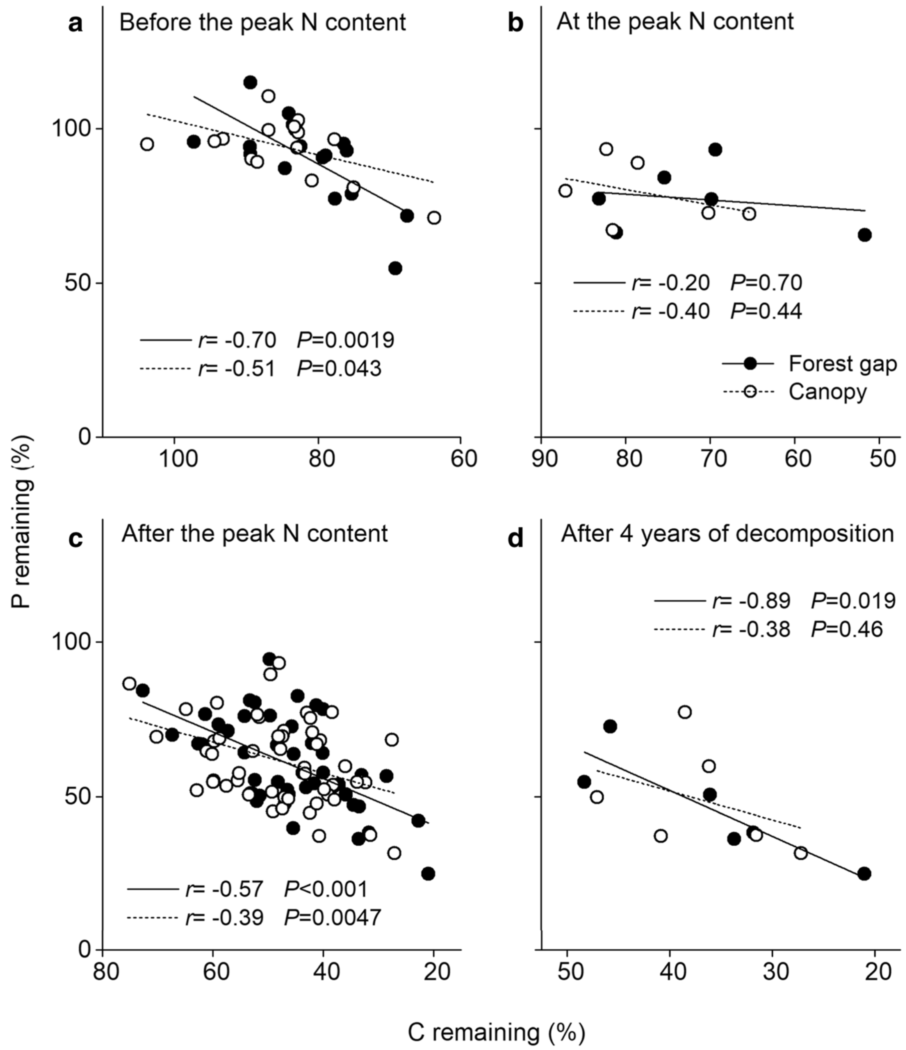

Fig. 9 Remaining carbon (C) versus remaining phosphorus (P). **a** Before the peak N content (n = 33). **b** At the peak N content (n = 12). **c** After the peak N content (n = 99). **d** After 4 years of decomposition (n = 12). Values are means (± SE, n = 6) for the six foliar litters in forest gaps and under canopy. Pearson's r and P values from linear regressions are shown in each panel. P values between forest gap and canopy plots from analysis of covariance were 0.47, 0.39, 0.61 and 0.98 for panels (**a**), (**b**), (**c**) and (**d**) respectively

during early periods of decomposition (Parton et al. 2007) and that an N/P ratio of 16 or a C/P ratio of 700 is important in determining P release (Moore et al. 2006). In this study, the N contents in fresh litters ranged from 0.67 to 1.3%, and 24–46% of N was retained in decomposing litters in the first year of decomposition. The initial N/P and C/P ratios ranged from 6.2 to 14.6 and from 408 to 544 (Table 3), respectively, resulting in P being consistently released from litter as C was lost. These results are consistent with previous long-term findings (Moore et al. 2006; Aerts et al. 2012). However, although these inter-site studies were conducted in multiple climate zones, most of them did not assess the inner-site differences in microclimate (Moore et al. 2011). Our study found that forest gaps decreased the peak N content and critical C/N ratio for some litter species (Fig. 5); such a decline in N retention led to the litter releasing more N and P during late periods of decomposition in this alpine forest.

Two potential mechanisms may explain the effect of forest gaps on N retention. First, the litter fall in forest gaps was only 12% of those in canopy areas in this alpine forest (Fu et al. 2017), which decreased the soil microbial assimilation of N from litter inputs. Therefore, soil microbial biomass has often been observed to be lower in forest gaps in many forests (Bauhus 1996; Ritter and Bjørnlund 2005; Schliemann and Bockheim 2014), and such a decline in microbial immobilization in forest gaps may decrease the critical C/N ratio, at which point the net release of nutrients begins (Manzoni et al. 2010). Second, numerous

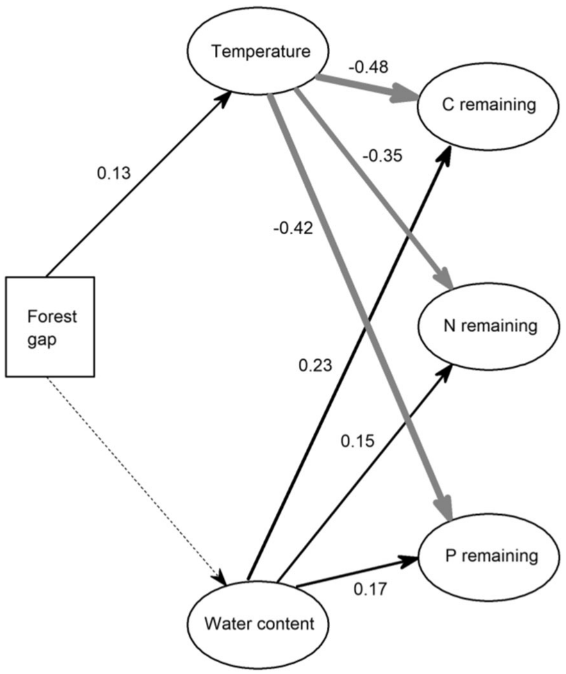

Fig. 10 Structural equation model showing the effects of forest gaps on litter temperature and water content. Solid and dashed arrows denote significant (black: positive, gray: negative; $P < 0.05$) and non-significant ($P > 0.05$) effects, respectively. Widths of arrows and associated numbers (standard regression weights) represent the strength of the path coefficients ($n = 864$). C: carbon, N: nitrogen, P: phosphorus

studies conducted over a wide range of biomes from tropical to boreal forests have demonstrated that formation of forest gaps greatly increased soil N mineralization and nitrification (Parsons et al. 1994; Ritter 2005; Scharenbroch and Bockheim 2007), resulting in more nitrate and ammonium leaching (Denslow et al. 1998; Prescott 2002; Prescott et al. 2003). Elevated available N in soils can also decrease the C/N threshold and lead to litter releasing more N and P during decomposition (Zechmeister-Boltenstern et al. 2015). These results have provided an important explanation of the uncertainty of the gap effect on litter decomposition and improved our current understanding of nutrient release patterns during litter decomposition as affected by the shifts in environmental conditions.

Soil temperature and moisture were directly changed after gap formation, but the effects of forest gaps on these factors varied greatly in different biomes, representing high uncertainty in assessing the gap effect. Overall, forest gaps may increase soil temperature in colder forests but decrease soil moisture in warmer biomes (Prescott et al. 2000); this may explain why the decomposition rates were observed to be higher in boreal forests (Bauhus et al. 2004; Lin et al. 2015) but lower in tropical and subtropical forests (Zhang and Zak 1995; González et al. 2014). In this studied alpine forest, winter snow cover and frequent freeze–thaw events were the two main environmental factors influencing litter decomposition (Wu et al. 2010; Ni et al. 2014). Snow cover accumulates more in forest gaps than under canopies and acts as an insulator on soil surface. The warmer environment beneath snow cover has been reported to increase microbial activity (Brooks et al. 1996) and to greatly contribute to nutrient release in cold biomes (Christenson et al. 2010; Saccone et al. 2013). Our results suggested that forest gaps had a greater effect on soil temperature than on litter water content and that temperature had stronger effect on the release of C, N and P than moisture (Fig. 10), suggesting that the stimulatory effect of forest gaps on C and nutrient release was primarily driven by the increase in temperature rather than in litter water content in this seasonally snow-covered forest. Thus, in addition to considering climatic factors across different biomes, variations in site microclimates induced by forest gaps can also modulate C and nutrient release from plant litter, and this should be considered as an important driver in regulating litter decomposition in seasonally snow-covered areas.

Conclusions

Decomposing litter initially retained N but immediately released P, and net N release began when the critical C/N ratio reached levels of 21–41 in litters in this alpine forest. Forest gaps showed a tendency to stimulate C and nutrient release from plant litter for some species (i.e., larch, birch and willow litters) during 4 years of decomposition resulted from the decline in N retention in gaps. This stimulatory effect of forest gaps was driven by the increase in temperature and not the water content of litter. These results suggest that formation of forest gaps during forest regeneration may accelerate C turnover and nutrient cycling and that this stimulation might be regulated by litter species in this seasonally snow-covered forest.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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