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# Global forest gaps reduce litterfall but increase litter carbon and phosphorus release



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Ongoing global climate change and conventional forestry have led to a dramatic increase in new forest gaps, predicted to strongly impact litter turnover and nutrient cycling. Here we synthesized 8739 paired observations to quantify the impacts of naturally occurring and artificially created gaps on litterfall, litter decomposition, and the release of carbon and nutrients. Globally, forest gaps decreased annual litterfall by 29.5% and litter remaining carbon and phosphorus by 5.6%, while litter decomposition increased in the 0–20% mass loss interval. Climate and litter quality showed a major contribution to forest gap effects on litter decomposition, with gap characteristics further influencing the release of carbon and nutrients during decomposition. Our results uncovered the potential impact of escalating forest gaps on reducing litter turnover and carbon sequestration, providing support for the inclusion of gaps into global litter dynamic models to improve predictions of ecosystem material cycling responses to ongoing climate change.

Climate-induced disturbances of forest ecosystems such as extreme drought or strong windstorms, as well as anthropogenic activities like logging and forest management, have shown large changes in forest canopy cover and continuity in recent years<sup>1–4</sup>. An increase in both the frequency and intensity of forest gap disturbances has been documented across the globe<sup>5–7</sup>. The change in gap disturbance affects the production and decomposition of litter, expected to be among the most important factors with a significant impact on forest ecosystems<sup>8,9</sup>. Litter input and its decomposition are inevitably influenced by forest gaps, due to their sensitivity to biotic and environmental factors<sup>10,11</sup>. Therefore, evaluating the effects of forest gaps on litter decomposition has major implications for the present and future of the global carbon pools and nutrient cycling in forest ecosystems<sup>12,13</sup>. However, the response of litter to forest gaps may vary among different forest types and climatic regions, and the underlying drivers and patterns of these variations remain unclear.

The consequences of forest gap disturbances on litter turnover are multifaceted, encompassing changes in litterfall and decomposition processes, along with the release of carbon and nutrients in the decomposing litter. Among them, litterfall as often calculated with annual or monthly litter production, is the beginning of the transfer of organic matter and nutrients from vegetation to soil<sup>14</sup>. The decomposition of litter with the release of elements can indicate the efficiency of material and energy transfer

processes in forests<sup>15</sup>. These elements include key plant constituents such as carbon (C), essential nutrients such as nitrogen (N), phosphorus (P), and potassium (K), trace elements like calcium (Ca), and magnesium (Mg), as well as primary C components like cellulose and lignin, which dominate in the whole stages of decomposition<sup>16–19</sup>. Forest gaps not only directly change the microclimatic conditions of the forest floor, redistribution and intensity of light, temperature, and precipitation, but also indirectly change the litter quality due to the changes in dominant vegetation<sup>20,21</sup>. On one hand, forest gaps may promote positive effects such as increased litterfall via the influx of plant remnants through the increased tree mortality<sup>22</sup> and elevated net primary productivity under improved irradiance and water availability<sup>23</sup>. Forest gaps may also accelerate litter decomposition due to the improvement of microclimatic conditions. For example, the opening of forest canopy increases soil temperature by allowing more solar radiation to reach the soil surface, reduces the interception of rainfall by canopy trees thus increasing soil moisture, and promotes the evaporation of soil moisture into the atmosphere due to the exposure of understory soil<sup>24,25</sup>. Litter decomposition is further facilitated by various biotic mechanisms such as enhanced microbial activity<sup>26</sup> and higher enzyme activity<sup>27,28</sup>. On the other hand, gap disturbances can potentially have negative effects on litterfall and litter decomposition due to reduced vegetation cover<sup>29</sup>, altered resource distribution<sup>30</sup>, decreased litter quality and soil decomposer activity<sup>31</sup>.

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Overall, a general consensus and theoretical framework still entail several challenges. For instance, previous studies indicated that litterfall and litter decomposition in forest gaps have been enhanced<sup>32</sup>, inhibited<sup>33</sup>, or unchanged<sup>34</sup>. Meanwhile, higher<sup>35</sup>, lower<sup>36</sup>, or similar<sup>37</sup> element releases in the decomposing litter were observed in the forest gap compared to those in the closed canopy.

Various responses of litterfall and litter decomposition to forest gaps have been observed globally<sup>38–40</sup>. The climate, which is widely recognized as a key driver of litter turnover at regional and global scales<sup>41–43</sup>, may further modify the responses of litterfall and litter decomposition to gap disturbance by determining forest gap formation and duration, temperature, precipitation, and their seasonal changes<sup>44–46</sup>. For example, forest gaps showed faster litter decomposition in arid regions<sup>47</sup> but slower litter decomposition in humid areas<sup>48</sup>. Forest type is another important factor, as differences in tree species composition and vegetation structure directly influence litter quality, light, and water accessibility<sup>49,50</sup>. A recent meta-analysis revealed the importance of maintaining gap edge trees, as clearances created by clear-cutting are no longer surrounded by gap edge trees, resulting in a significant reduction in litter decomposition rates<sup>51</sup>. According to previous studies, the effects of forest gap on litter decomposition and nutrient release could be higher in broadleaved forests than in coniferous forests<sup>52,53</sup>. In addition, some studies<sup>54,55</sup> showed that larger natural forest gaps could increase sunlight, raise soil temperatures, and promote vegetation diversity by providing more living space, as well as creating microclimates suitable for litter decomposition through edge effects near the closed canopy. In contrast, other studies<sup>56,57</sup> proposed that the drier conditions, nutrient leaching, and vegetation weakening associated with larger gaps could conversely limit litterfall and litter decomposition. Unfortunately, the relative importance of these drivers remains unknown, due to the various experimental manipulations at the broad range of climate conditions and various forest types which can modulate the response of litter turnover. Therefore, exploring the explicit patterns of forest gap disturbances on litter and further identifying the key drivers will provide a first insight into the ecosystem material cycle under the changing climate scenario.

Based on the field data collection as well as data search of published data globally, we conducted a meta-analysis to synthesize 8739 observations. The main objective was to evaluate the global patterns, temporal dynamics, and key drivers underlying the effects of forest gaps on litterfall, litter decomposition, and element release. Building upon our decade-long observational study (2010 to 2020) of the impact of forest gaps on litter decomposition in an alpine forest, we propose the following hypotheses: (1) forest gaps would inhibit the accumulation of litterfall while enhancing litter decomposition, resulting in a positive effect on element release during the decomposition process; (2) climate conditions might be the main driver of the forest gap effects, and the effects on litter decomposition could vary among different climatic regions. The results can be expected to quantitatively integrate the global effects of forest gaps on a range of dynamic processes from litterfall to decomposition and element release, providing a better understanding of material cycling in forest ecosystems under widespread gap disturbances.

## Results

### Overall effects of forest gaps

Overall, the presence of forest gaps significantly decreased litterfall by 29.5% (CI: 7.4–46.3%) but showed few significant effects on litter decomposition rate and mass loss. Forest gaps caused a significant reduction in the remaining litter C and P by 5.6% (CI: 0.9–10.1%) and 5.6% (CI: 1.0–10.0%), respectively. Nevertheless, the overall effect was not statistically significant on the remaining N, K, Ca, Mg, cellulose and lignin during litter decomposition (Fig. 1). The effect of forest gaps on litter mass loss, as well as the remaining C, N, P, and K, varied across different stages of decomposition. Forest gaps supported litter decomposition in the less than 20% mass loss interval, although this significantly reduced remaining C and P in the 20–80%, N in the 0–10%, and K in the 40–70% mass loss intervals during litter decomposition (Fig. 2).

### Effects of forest gap characteristics

Forest gap characteristics, including gap age, size, and location, as well as canopy tree phenology and leaf type, displayed no differences among their respective categories in the gap effects on litterfall (Fig. 3a). However, the effects of forest gap on litter decomposition significantly varied with gap sizes and canopy tree phenology, showing 7.1% and 19.8% increases in mass loss in small gaps (diameter  $\leq 15$  m) and deciduous forests, respectively (Supplementary Fig. 1). Similarly, the impacts of the forest gap on the remaining C and P were regulated by gap sizes and locations, and the remaining N and K were regulated by gap locations (Fig. 3b; Supplementary Fig. 1). In addition, artificial gaps respectively decreased 23.8% and 10.6% of the remaining cellulose and lignin in decomposing litter, whereas natural gaps exhibited few effects (Supplementary Fig. 1).

### Effects of climate, litter quality, and experimental conditions

Climate primarily drives the effects of forest gaps on litter decomposition rather than on litterfall. The decomposition rate increased by 37.1% in arid areas, and mass loss increased by 19.5% and 9.3 in arid and cold areas, while the remaining K decreased by 13.6% in polar areas (Fig. 4a, b; Supplementary Fig. 2). The impact of forest gaps on litter decomposition rate and mass loss exhibited a negative response to MAP (Table 1). Litter types showed close relationships with the effects of gaps, which increased decomposition rate, mass loss, and remaining C and N in branch litter while decreasing remaining C and N in leaf litter (Fig. 4a–d). Furthermore, the effects of gaps on decomposition rate and remaining K showed significant responses to initial lignin concentration. The remaining N, K, and cellulose in decomposing litter responded positively to the initial C:N ratio, while the remaining Ca responded negatively to the C:N ratio (Table 1; Supplementary Table 1). In addition, litterbag mesh positively impacted the remaining cellulose during litter decomposition (Table 1). Among them, climate and litter types emerged as the most crucial drivers in checking the effect of forest gaps on decomposition (Supplementary Table 2).

## Discussion

Our global analysis provides convincing evidence that forest gaps reduce litterfall while showing few significant effects on litter decomposition. These findings align with part of our hypothesis, as we observed a positive effect of gaps on litter C and P release during litter decomposition. Although overall decomposition rates were not significantly altered by forest gaps, positive effects were discerned in the early stages of decomposition. Importantly, the effect of forest gaps on litter decomposition was equally affected by climatic region and litter type, and the release of elements during the decomposition process was further affected by gap characteristics (Fig. 5). The formation of forest gaps and their effects on element release support previous findings<sup>58</sup>, with more significant effects in artificial gaps than in natural gaps. Similarly, our results are supported by a recent meta-analysis<sup>59</sup>, which found that soil P is increased by gap disturbance, especially in coniferous forest plantations. Here, faster woody plant regeneration may be attributed to the heightened release of nutrients from litter.

The litterfall was negatively affected by forest gaps at the global scale. In addition, litterfall showed a negative response across various gap characteristics, regardless of climate. This finding highlights the widespread ecological significance of reduced litterfall as a consequence of forest gaps. Some possible explanations suggest a decrease in productivity attributed to reduced tree vegetation within gaps<sup>60</sup>, alterations in plant composition<sup>61</sup>, the heightened vulnerability of the forest floor to direct rainfall<sup>62</sup>, and shifts in the feeding activity and abundance of herbivores and decomposers<sup>63</sup>. This ecological mechanism has the potential to disrupt nutrient cycling and carbon storage within forest ecosystems<sup>64</sup>. Specifically, one anticipated outcome of increasing forest gaps is the reduction in nutrient availability for plant uptake and utilization of nutrients, potentially constraining plant growth and forest productivity<sup>65</sup>. Furthermore, the decline in litterfall may impact soil organic matter accumulation and alter microbial communities participating in decomposition processes<sup>66</sup>. These findings collectively suggest that forest gaps could result in adverse ecological effects, including

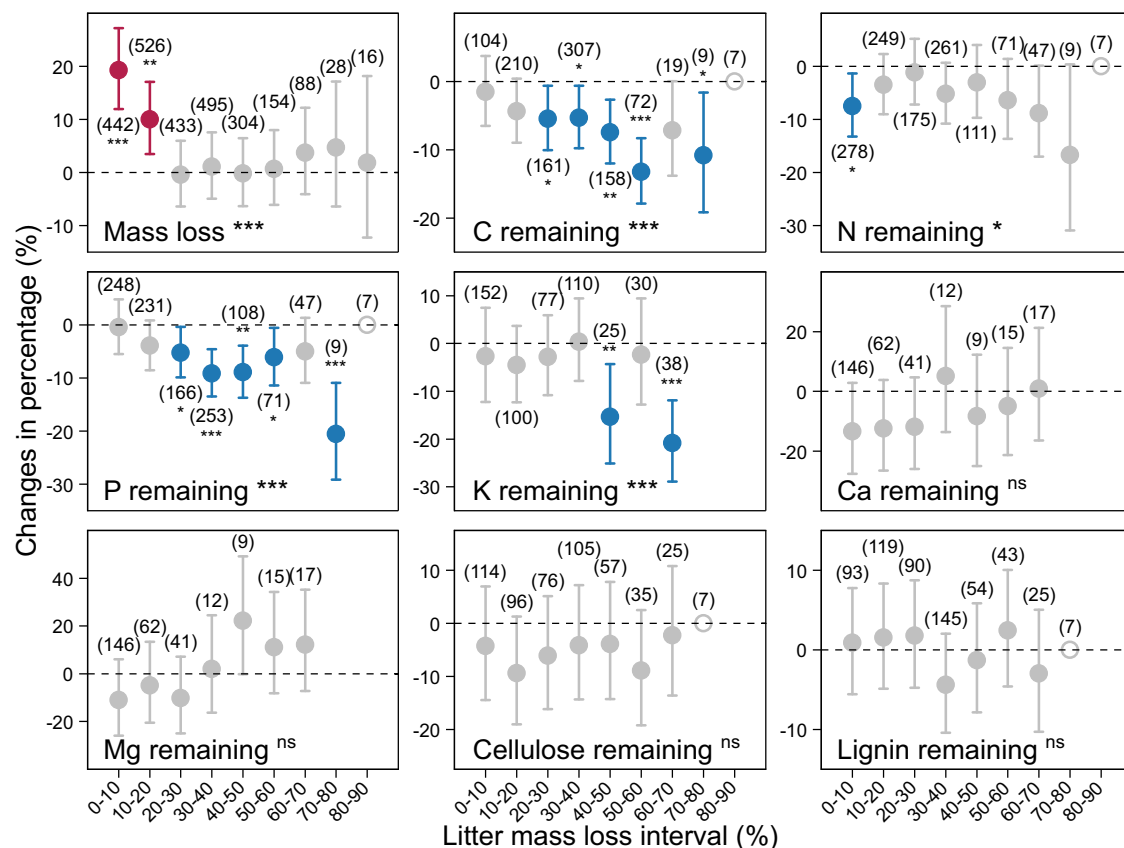
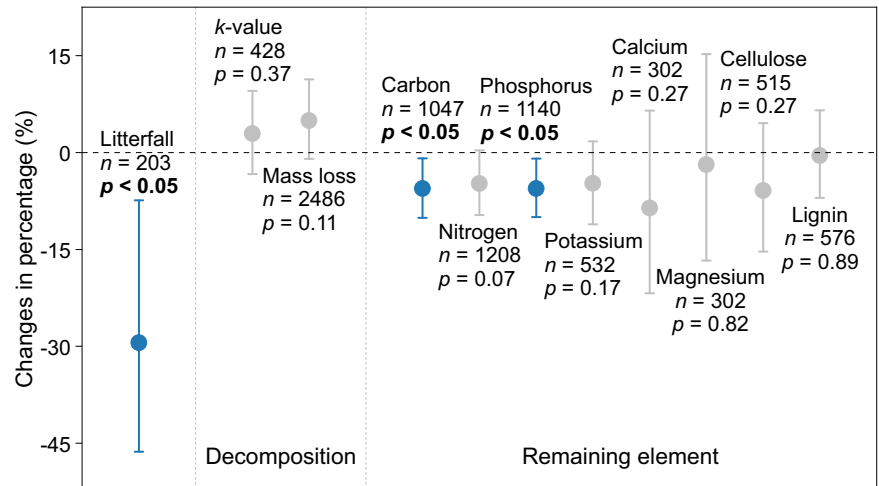
diminished vegetation coverage and biodiversity, thereby contributing to the observed decrease in litterfall.

In contrast to the global negative effects on litterfall, the impact of forest gaps on litter decomposition indicated diverse patterns, with the most significant effects shown in the early stages. Initially, forest gaps expose litter to external factors such as physical fragmentation which in turn provide light and space, attract more decomposers, and thus enhance their activity<sup>12</sup>. Moreover, litter decomposition in gaps within deciduous forests responded

positively to gaps, where higher resource concentration and reduced competition are due to continuous organic matter supply from seasonal defoliation<sup>67</sup>. These positive effects create a favorable environment for the decomposition and transformation of complex organic compounds by soil microbes and animals<sup>21</sup>.

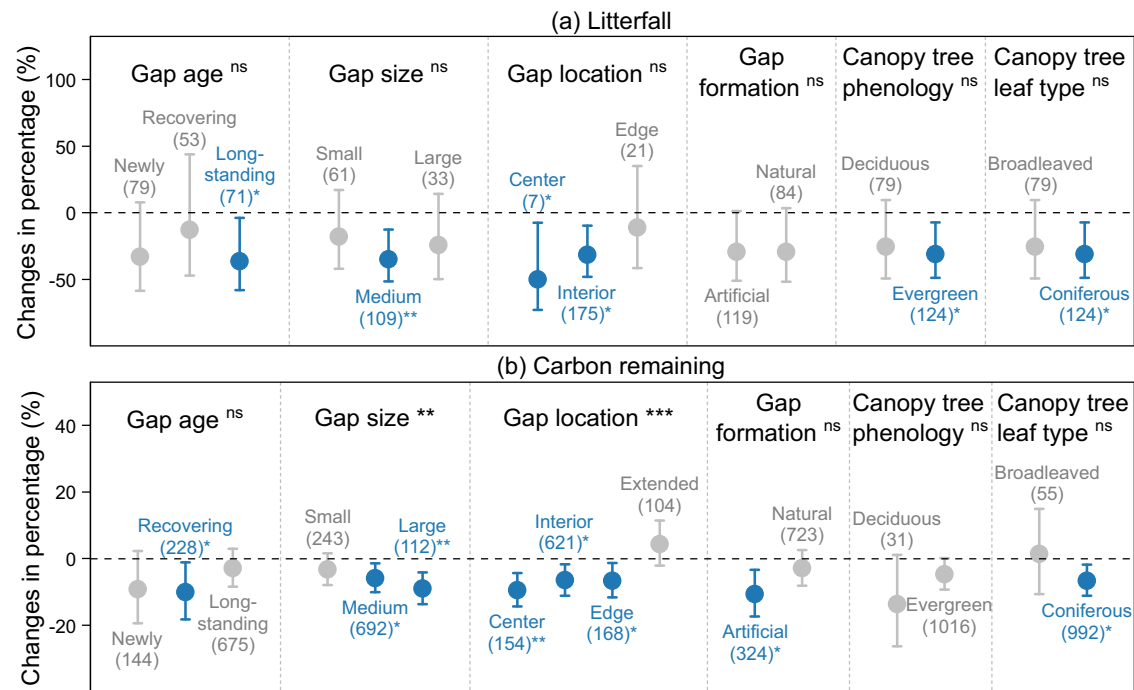
Interestingly, the effects of forest gaps varied significantly across different climatic regions, while we also observed a decrease in litter decomposition with higher MAP. Two simultaneous processes during litter

**Fig. 1 | Overall effects of forest gaps on litterfall, litter decomposition rate ( $k$ -value), mass loss, and remaining elements.** Values indicate means with 95% confidence intervals, the number of paired observations ( $n$ ), and the significance levels ( $p$ ) from linear mixed-effects models. Blue symbols represent significant negative effects, while gray symbols indicate non-significant results.



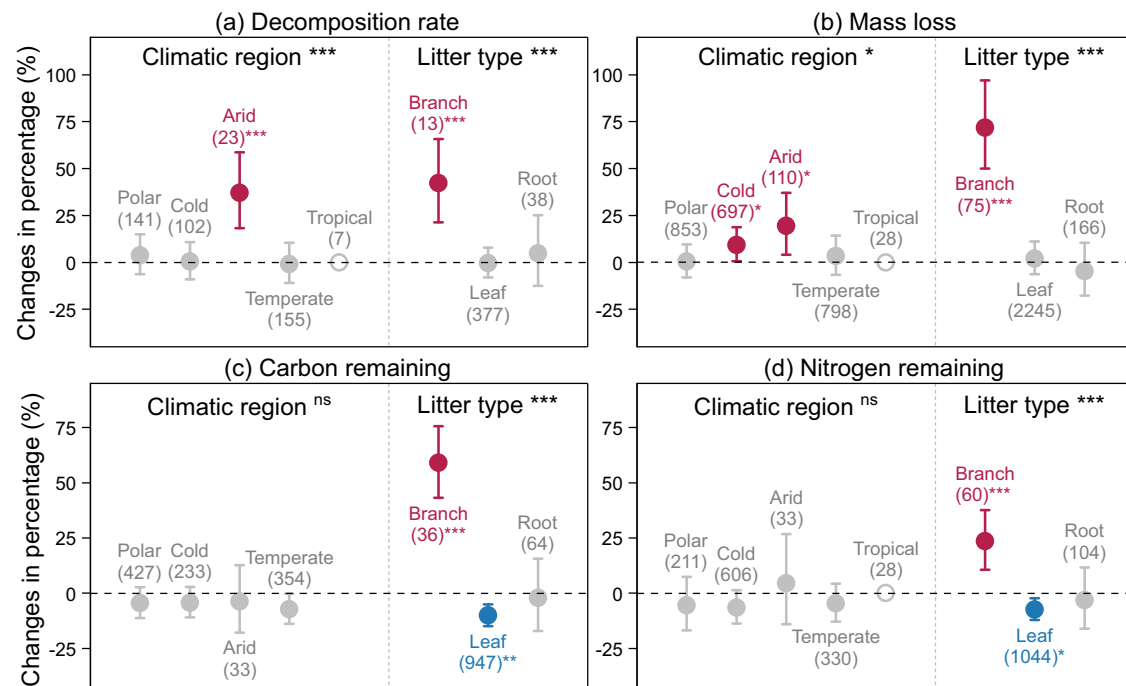
**Fig. 2 | The effects of forest gaps on litter mass loss and remaining elements over the stages of decomposition (0–90% mass loss, data for the 90–100% interval are unavailable).** C: carbon, N: nitrogen, P: phosphorus, K: potassium, Ca: calcium, Mg: magnesium. Values indicate means with 95% confidence intervals, and the number of paired observations is shown in parentheses. Superscripts following the variables

indicate the significance of differences between various mass loss intervals. Red and blue symbols indicate significant positive and negative effects, while gray symbols and "ns" indicate statistically non-significant results. Hollow symbols indicate observations from a single study that cannot be included in the analysis. Significance levels are denoted as \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .



**Fig. 3 | The effects of forest gap characteristics.** The effects of forest gap characteristics on litterfall (a) and remaining carbon (b) were assessed using a linear mixed-effects model (Refer to Supplementary Fig. 1 for decomposition and remaining nutrients). Values indicate means with 95% confidence intervals, and the number of paired observations is shown in parentheses. Superscripts following the

category names of categorical variables indicate the significance of differences within each category. Blue symbols indicate significant negative effects, while gray symbols and “ns” represent statistically non-significant results. Significance levels are denoted as \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .



**Fig. 4 | The effects of climatic region and litter type.** The effects of climatic region and litter type on the response of litter decomposition rate (a), mass loss (b), remaining carbon (c), and nitrogen (d) to forest gaps were evaluated using a linear mixed-effects model (refer to Supplementary Fig. 2 for litterfall and other remaining nutrients). Values indicate means with 95% confidence intervals, and the number of paired observations is shown in parentheses. Superscripts following the category

names of categorical variables indicate the significance of differences within each category. Red and blue symbols indicate significant positive and negative effects, while gray symbols and “ns” represent statistically non-significant results. Hollow symbols indicate observations from a single study that cannot be included in the analysis. Significance levels are denoted as \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Table 1 | The effects of climate, initial litter quality, and experimental condition on the response of litter decomposition rate (*k*-value), mass loss, remaining potassium, calcium, and cellulose to forest gaps (refer to Supplementary Table 1 for litterfall and remaining carbon and other nutrients)**

Predictor	Decomposition		Remaining element		
	<i>k</i> -value	Mass loss	Potassium	Calcium	Cellulose
<i>Climate</i>					
Elevation	0.11	−0.03	−0.01	−0.11	0.10
MAT	0.06	−0.02	−0.33	0.30	−0.45
MAP	−0.34**	−0.25*	−0.21	0.08	0.09
<i>Initial litter quality</i>					
C:N ratio	−0.02	0.09*	0.26***	−0.16*	0.43***
Lignin concentration	−0.18**	−0.06	0.22*	0.06	−0.02
<i>Experimental condition</i>					
Litterbag size	−0.03	−0.13	0.25	0.18	0.94
Litterbag mesh	0.02	0.02	−0.02	−0.03	−0.10*

MAP mean annual precipitation, MAT mean annual temperature, C carbon, N nitrogen.

Results are estimates of fixed effects from linear mixed-effects models, with asterisks indicating significant effects (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

decomposition, involving microbial activities and the leaching of soluble substances, could be closely related to the observations<sup>68,69</sup>. In arid climates, the positive impact of gaps could be associated with the relief from moisture stress, creating conducive conditions for decomposition<sup>70</sup>. By contrast, in tropical climates, the inherently high temperatures and humidity may exacerbate the negative effects of forest gaps on the biological participants in decomposing litter<sup>71</sup>. High precipitation fills the pores in the litter with water, slowing its breakdown by creating an anoxic environment and restraining microbial metabolism<sup>72</sup>. Likewise, litter type emerges as another principal driver, with initially higher carbon and lower lignin concentrations resulting in faster decomposition. The enhanced microbial colonization, which could be supported by improved microclimatic conditions, facilitates a more positive effect of gaps on branch litter<sup>73</sup>.

Forest gaps primarily promote the release of C and P during litter decomposition. This positive impact persists throughout the later stages of litter mass loss. While the early stages experience accelerated litter decomposition facilitated by forest gaps, the delayed release of nutrients could be attributed to heightened microbial adaptability and the breakdown of recalcitrant compounds over time<sup>74,75</sup>. Similarly, the higher release of nutrients, including P, Ca, and Mg, in small gaps reaffirms the obvious advantages of small-scale canopy openings. These gaps exhibit greater ecological resilience owing to their adaptability and responsiveness to external pressures<sup>23</sup>.

However, higher litter C releases were observed in larger gaps, along with concentrated releases of nutrients like P and K at the gap center, where decomposition may be more rapid and efficient. This process may reflect poorer soil properties in larger gaps due to the continuous reduction of nutrient supply from living plants, as well as increased nutrient demand due to increased living space promoting vegetation regeneration. As a result of it, increased nutrient release from litter may be desirable for vegetation restoration and increased soil fertility in larger gaps. Specifically, alterations in the microenvironment caused by gaps could make litter more accessible as a nutrient source. Increased sunlight input stimulates greater nutrient requirements for vegetation growth and decomposing activity<sup>76</sup>. Furthermore, N and P are released more at the gap edges, combining characteristics of both environments to create a more favorable ecological setting for nutrient release by decomposing litter<sup>77</sup>. In artificial gaps, recalcitrant compounds such as cellulose and lignin degrade more quickly, implying that

mechanical soil alteration after artificial cutting may promote the decomposition process of leaf litter<sup>51</sup>. This finds explication in a confluence of factors, first, microsite disturbances from trampling and vegetation clearance during gap formation<sup>78</sup>, second, the intentional spatial distribution of artificial gaps<sup>79</sup>, and third, the relatively homogenous species composition and higher density in artificial forests<sup>80</sup>. These factors create conditions favoring nutrient release in the litter, indicating that simulating forest gaps in artificial forests benefits vegetation in nutrient acquisition.

The impacts of various litter types and initial quality on C and nutrient response to forest gaps emphasize the importance of decomposable substrates in predicting subsequent nutrient dynamics. For example, the higher initial N in litter serves as an original nutrient stimulus, promoting nutrient effectiveness in the gap environment<sup>81</sup>. In contrast, branch litter with higher initial lignin demonstrates limited nutrient release, possibly attributed to the slower decomposition rates associated with recalcitrant compounds<sup>82</sup>. In addition, the degradation of cellulose increased with the litterbag mesh, potentially serving as a valuable indicator of the important role played by soil fauna in the decomposition process within forest gaps<sup>83</sup>.

The results of our meta-analysis provide valuable insights into the effects of forest gaps on litter dynamics and nutrient cycling in forest ecosystems. However, further research is needed to address certain limitations. Firstly, the limited availability of studies on bark litter and the methodological differences in studying wood litter prevented their inclusion in our analysis. Future research should focus on including a wider range of litter types and employ comparable methodologies such as mass loss ratio, decomposition index, and litter quality index to facilitate more comprehensive comparisons. Secondly, the limited availability of data on late-stage or limit-value stages hindered our ability to analyze element release dynamics. However, interesting trends were observed in our limited dataset for recalcitrant components such as cellulose and lignin. Collecting more data during these decomposition periods will provide valuable insights into the dynamics of recalcitrant component changes and their influence on nutrient cycling.

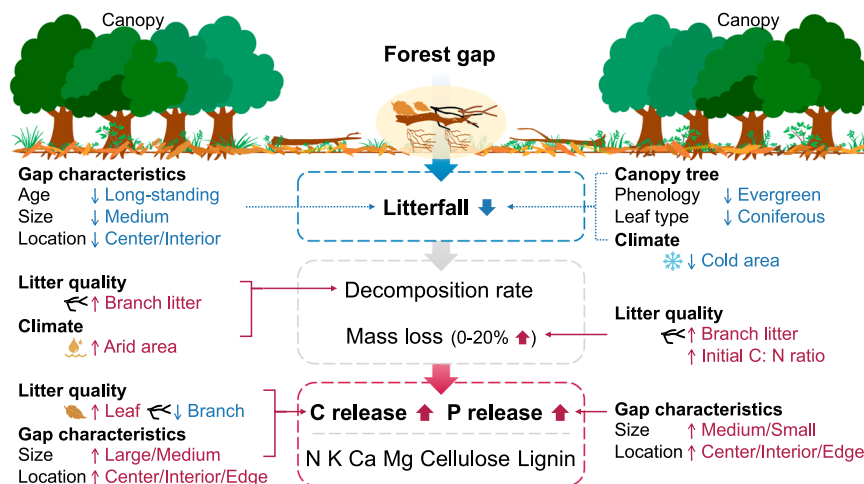
Moving forward, future research should focus on exploring the optimal size of forest gaps for nutrient cycling, investigating the interactions between elements during litter decomposition, and considering the combined effects of factors influencing litter input and decomposition on annual litter turnover. Moreover, it is important to analyze changes in microbial communities involved in the transformation<sup>84</sup> and decomposition of leaf and wood litter in various forest gaps, which would require combining different advanced methods such as amplicon sequencing techniques and stable isotope probing methods<sup>85</sup>. Furthermore, we should not ignore soil fauna which play a significant role in litter decomposition and transformation of plant residuals<sup>83</sup>, as this may vary between gaps depending on the abundance and diversity of soil organisms. In addition, measuring greenhouse gas emissions under the influence of forest gaps on litter decomposition may also be an issue worth considering, as they may reflect the carbon balance of the forest ecosystem. These efforts will contribute to a more comprehensive understanding of nutrient cycling and inform effective management strategies for forest ecosystems.

## Conclusions

In conclusion, our study addresses a critical gap in current forest disturbance research, presenting the first comprehensive analysis of global forest gap effects and drivers on litterfall, litter decomposition, and element release. Our findings clearly demonstrate a positive effect of forest gaps on litter decomposition in the 0–20% mass loss interval, and this effect is equally driven by climatic region and litter type. Moreover, our study reveals that forest gaps increase C and P release during litter decomposition, regulated by the same drivers as the decomposition and further affected by gap characteristics such as size and location. Concerning recalcitrant components, the positive effect is particularly conspicuous in artificial gaps and larger litterbag mesh, where an increase in lignin degradation was observed. In addition, these findings emphasize the potential consequences of escalating gap disturbances on carbon emissions and nutrient release, bearing



**Fig. 5 | Schematic diagram of the effects and drivers of forest gaps on litterfall, decomposition, and the release of carbon and nutrients.** The red and blue arrows represent significant positive and negative effects. C: carbon, N: nitrogen, P: phosphorus, K: potassium, Ca: calcium, Mg: magnesium.



implications for ecosystem material cycling in the context of climate change. However, irrespective of gap characteristics or climatic region, our results consistently demonstrate a global decline in litterfall due to forest gaps, posing a challenge to litter turnover. These results highlight the importance of including forest gaps in global dynamic models of litter decomposition to explore the mechanisms and improve predictions of ecosystem material cycling responses to ongoing climate and vegetation change.

## Methods

### Data collection and database compilation

We conducted a comprehensive search on the Web of Science (<http://webofknowledge.com>) and China National Knowledge Infrastructure (<http://www.cnki.net>) for peer-reviewed journal articles and academic papers published before March 30, 2024, focusing on the effect of forest gaps. The literature search utilized a combination of the following terms: (“forest gap” OR “canopy gap” OR “treefall gap” OR “gap size” OR “gap dynamics” OR “canopy opening” OR “tree mortality” OR “tree death” OR “forest mortality”) AND (litter OR detritus OR leaf OR foliar OR bark OR branch OR root OR wood OR twig). To be included in our database, studies must meet the following criteria: (1) data obtained from field experiments, wherein control and forest gap treatments are established in forest microsites under identical conditions; (2) forest gap treatments must report the specific area of the closed space formed by gap edge trees together, excluding clear-cutting treatments that are not surrounded by gap edge trees, partial canopy removal treatments that do not create real aggregation gaps such as canopy trimming, thinning and shelterwood interventions, and simulated gap treatments using artificial shade structures; (3) collection of litterfall data reflecting the average annual total litterfall; (4) litter decomposition studies should utilize the litterbag method, decomposition times must be explicitly reported, and the variables related to element release during litter decomposition must be matched with litter mass loss data from the same site, in order to investigate the impact of forest gaps on litter mass and elements over the stages of decomposition; (5) only control and forest gap treatment data are used in multifactorial studies.

Based on these criteria, we obtained 8739 observations from 82 publications (Supplementary Fig. 3 and Supplementary References), including ~30% of the case studies conducted by our group during the period from 2010 to 2020. Specifically, 24 publications reported 203 pairs of mean observations of average annual litterfall ( $\text{g m}^{-2} \text{ year}^{-1}$ ) in gap treatment and control groups, with about 58% of case studies using litter traps for litter collection, and 42% using quadrat methods for direct investigation. As for litter decomposition, 51 publications reported 2486 pairs of mean observations of litter mass loss (%) in the gap treatment and control group. A total of 428 pairs of decomposition rates ( $k$ -value) were calculated based on mass

loss. The  $k$ -value of litter was estimated using a single exponential model<sup>86</sup>:

$$k = -\frac{1}{t} \ln(M_t/M_0) \quad (1)$$

where  $M_0$  is initial litter mass,  $M_t$  is remaining mass at sampling time  $t$  (year). Elemental release during litter decomposition includes remaining C (1047 pairs of mean observations from 21 publications), nitrogen (1208 pairs of mean observations from 27 publications), phosphorus (1140 pairs of mean observations from 23 publications), potassium (532 pairs of mean observations from 12 publications), calcium (302 pairs of mean observations from 7 publications), magnesium (302 pairs of mean observations from 7 publications), cellulose (515 pairs of mean observations from 9 publications), and lignin (576 pairs of mean observations from 10 publications). The element remaining ( $R_t$ ) can be calculated based on the element concentration and litter mass:

$$R_t = \frac{C_t \times M_t}{C_0 \times M_0} \times 100\% \quad (2)$$

where  $M_0$  and  $C_0$  are initial litter mass and initial element concentration, respectively.  $M_t$  and  $C_t$  are remaining mass and element concentration at sampling time  $t$  (year), respectively. Due to the different time intervals measured by decomposition studies, we use a classification based on the mass loss to assign different studies to the same decomposition stage<sup>87</sup>, by dividing the data into 10% mass loss intervals (0–10, 10–20, ... 80–90%, except for unavailable 90–100% interval). Then, to quantify the drivers of forest gaps on litter, we collected data on forest gap characteristics, climatic factors, litter quality, and experimental conditions. Each variable in our analysis was extracted from multiple studies, while observations from single studies were collected but not incorporated into the analysis.

For the classification of effect factors, our categorization was based on the following criteria: (1) forest gap ages was classified based on the gap-closure standard (with a mean value of 14.5 years) proposed by Lu et al.<sup>88</sup>, dividing into newly formed gaps (up to and including 1.0 year old), recovering gaps (between 1.0 and 14.5 years old), and long-standing gaps (more than 14.5 years old); (2) forest gap sizes were categorized with reference to the classification proposed by Zhu et al.<sup>89</sup>, which is based on the ratio of forest gap diameter to the average height of tree canopies, but due to limited information on tree canopy height in the original studies, the classification was predominantly determined by gap diameter, encompassing small gaps (diameter  $\leq 15$  m), medium gaps (15 m < diameter  $\leq 30$  m), and large gaps (diameter > 30 m); (3) forest gap formation was categorized as natural or artificial, natural formation includes factors such as storms, windstorm, natural mortality, and drought, while

artificial formation was mainly created by cutting and selective logging, the varying formation often result in different gap sizes, so we have not made further subdivisions; (4) forest gap locations were divided into the gap center, gap interior (the ground area below the opening of the tree canopy), gap edge (position directly below the opening of the tree canopy), and extended gap edge (adjacent area extending around the gap from the bottom of the tree canopy); (5) canopy tree phenology were classified as deciduous and evergreen; (6) canopy tree leaf types were classified as broadleaved and coniferous; (7) climatic region were determined based on the present Köppen-Geiger climate classification<sup>90</sup>, including tropical, temperate, arid, cold, and polar areas; (8) litter types include branch, leaf, and root litter.

For continuous effect factors, we considered the effects of elevation (m), mean annual temperature (MAT, °F), mean annual precipitation (MAP, mm), initial litter C:N ratio, initial lignin concentration (%), litterbag size (cm<sup>2</sup>), litterbag mesh size (mm). The data were obtained from the primary text, tables, and appendices, or digitized from figures using Engauge Digitizer version 12.1 (Free Software Foundation, Inc.). In cases where data were not provided, we obtained elevation, MAT, and MAP data from the WorldClim v.2 databases<sup>91</sup>.

### Data analyses and statistics

We employed linear mixed-effects models using the *lme4* package in R software to test the effects of forest gaps on litter and the contribution of drivers<sup>92</sup>. To quantify the overall effects of forest gaps on litterfall, decomposition, and element release, we used natural log-response ratio (ln RR)<sup>93</sup>. Each paired observation of ln RR was calculated as follows:

$$\ln RR = \ln(\bar{X}_t / \bar{X}_c) \quad (3)$$

where  $\bar{X}_t$  and  $\bar{X}_c$  were the means of the forest gap treatment group and the canopy control group, respectively. For each response variable, we first ran an intercept-only model to estimate the overall average effect size of individual ln RR (ln RR<sub>++</sub>), treating study identity as a random effect, explicitly accounting for potential autocorrelation among individual study observations. Next, to evaluate the potential effects of predictors on the response of litter variables to forest gaps, we used linear mixed-effects models by fitting each predictor as a fixed-effects factor<sup>94</sup>. We included forest gap characteristics, climate factors, litter quality, and experimental conditions as fixed-effect factors, either as continuous or categorical variables. Continuous variables were log<sub>10</sub>-transformed before analysis to enhance the reliability and interpretability of the statistical results<sup>87</sup>. We used the Kenward-Roger approximation to test the statistical significance of these continuous and grouped fixed-effect terms, and further used the analysis of deviance table (Type II Wald Chi-Square tests) of the linear mixed-effects model to test the significance of differences within the groups. For ease of interpretation, the inverse transformation of the percentage change of ln RR<sub>++</sub> and its corresponding 95% confidence interval (CI) was as follows:

$$\text{Percentage change} = (e^{\ln RR_{++}} - 1) \times 100\% \quad (4)$$

if the 95% CI does not overlap with zero, it indicates a significant effect of forest gaps on litter. To further assess the relative importance of predictors that showed significant impacts on the response of litter variables to forest gaps, we employed mixed-effects meta-regression model selection using the *glmulti* package in R software<sup>95</sup>, based on maximum likelihood estimation. Before performing model selection, we initially employed the variance inflation factor (VIF) from the *car* package in R software to detect any potential covariance among the predictors that were integrated into the model, and the predictors were included in the model if their VIF < 5<sup>96,97</sup>. The importance of each effect factor was computed as the sum of Akaike weights across all models that included the effect factor, with a threshold value of 0.8 to discriminate between essential and non-essential predictors<sup>98,99</sup>. All data analyses were conducted in R version 4.3.1.

### Data availability

Data are available from the Figshare <https://doi.org/10.6084/m9.figshare.25754256.v2><sup>100</sup>.

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## Author contributions

X.Z. and F.W. conceived the study. X.Z. collected the raw data. P.H. and K.Y. organized the methods. X.Z. performed data analyses and wrote the original draft. F.W., P.H., and K.Y. wrote, reviewed, and edited the manuscript. X.N., X.W., Z.C., and J.Y. contributed to revisions of the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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