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The decomposition of dead organic matter is a major determinant of carbon and nutrient cycling in ecosystems, and of carbon fluxes between the biosphere and the atmosphere[1–3]. Decomposition is driven by a vast diversity of organisms that are structured in complex food webs[2,4]. Identifying the mechanisms underlying the effects of biodiversity on decomposition is critical[4–6] given the rapid loss of species worldwide and the effects of this loss on human well-being[7–9]. Yet despite comprehensive syntheses of studies on how biodiversity affects litter decomposition[4–6,10], key questions remain, including when, where and how biodiversity has a role and whether general patterns and mechanisms occur across ecosystems and different functional types of organism[4,9–12]. Here, in field experiments across five terrestrial and aquatic locations, ranging from the subarctic to the tropics, we show that reducing the functional diversity of decomposer organisms and plant litter types slowed the cycling of litter carbon and nitrogen. Moreover, we found evidence of nitrogen transfer from the litter of nitrogen-fixing plants to that of rapidly decomposing plants, but not between other plant functional types, highlighting that specific interactions in litter mixtures control carbon and nitrogen cycling during decomposition. The emergence of this general mechanism and the coherence of patterns across contrasting terrestrial and aquatic ecosystems suggest that biodiversity loss has consistent consequences for litter decomposition and the cycling of major elements on broad spatial scales.

Biological diversity that directly influences litter decomposition exists at multiple trophic levels[4]. This diversity includes plants that produce litter mixtures of varying quality, microbial decomposers and invertebrate consumers of varying body size, the last two of which selectively use the heterogeneous resources provided by litter mixtures[4,13]. General principles of the effects of biodiversity on litter decomposition have proved elusive: both pioneering work[14] and recent syntheses have highlighted contrasting effects of litter species richness on decomposition[4–6,15,16]. In part, this variation appears to be due to site-specific conditions, including contrasts between aquatic and terrestrial ecosystems, as well as between geographic settings. Further differences may arise from variation in experimental protocols, the plant species studied and the types of decomposers included in a given experiment. Such methodological discrepancies have complicated syntheses across studies, hindering the emergence of common patterns and mechanisms.

Here we report the results of the first concerted experiments studying the effects of biodiversity on decomposition by manipulating diversity across trophic levels and distinct biomes in both forest floor and stream habitats (Extended Data Table 1). We proposed that the functional diversity of decomposers (variation in body size) and of leaf litter (variation in litter quality) promotes C and N cycling across contrasting locations (subarctic to tropical) and ecosystem types (terrestrial versus aquatic). Body size encapsulates numerous species traits that are relevant to ecosystem functioning, and extinction scenarios project that the larger species will be preferentially lost from biological communities[17,18]. Similarly, plant functional types reflect differences in leaf quality traits that determine litter decomposition independently of geographical location[19]. Plant functional types are defined here in terms of plant C allocation strategies (deciduous versus evergreen), N acquisition strategies (N-fixing versus non-N-fixing) and litter recalcitrance (rapidly decomposing versus slowly decomposing) (Extended Data Table 2).

Mixing leaf litter from various plant functional types together resulted in accelerated C and N dynamics, as indicated by the overall net positive effects on C and N loss (that is, increased C and N loss with increasing functional diversity) (Fig. 1, C loss; Extended Data Fig. 1, N loss; $P < 0.05$, C and N loss). However, C loss from litter mixtures was only 2.9 ± 0.8 mg g^{-1} (mean $\pm$ s.e.m.) of initial litter dry mass greater than the expected loss based on data from single litter functional types, indicating only a modest increase in C cycling as a result of litter mixing. Although also statistically significant ($P < 0.01$), the difference in the loss of N across all litter mixtures was very small (0.1 ± 0.2 mg N g^{-1} of initial litter dry mass; mean $\pm$ s.e.m.; Extended Data Fig. 1). The net litter diversity effect on C loss was stronger in terrestrial than in aquatic ecosystems ($P < 0.001$, Fig. 1 and Extended Data Table 3), supporting theoretical predictions[4] but contrasting the results of a meta-analysis in which diversity effects on decomposition were significant only for streams[6]. Sorting the litter mixtures into species at the end of the experiments enabled us to explore potential reasons for this discrepancy, by partitioning the net diversity effects into complementarity effects (that is, the effects resulting from synergistic or antagonistic interactions) and selection effects (that is, the effects arising when the presence of a particular functional type with high (or low) process rates dominates a mixture)[20]. The observed net diversity effects were clearly driven by complementarity effects that were stronger than selection effects (Fig. 1). Overall, the complementarity effect was a similar strength to the net effect for C loss (3.4 ± 0.9 mg C g^{-1}), and even stronger than the net effect for N loss (1.0 ± 0.2 mg N g^{-1}). By contrast, the mean selection effects were not significant. The characteristics of the forest floor habitat that may favour complementarity effects include strong fluctuations in temperature and humidity and a homogenous litter cover[4]. Conversely,

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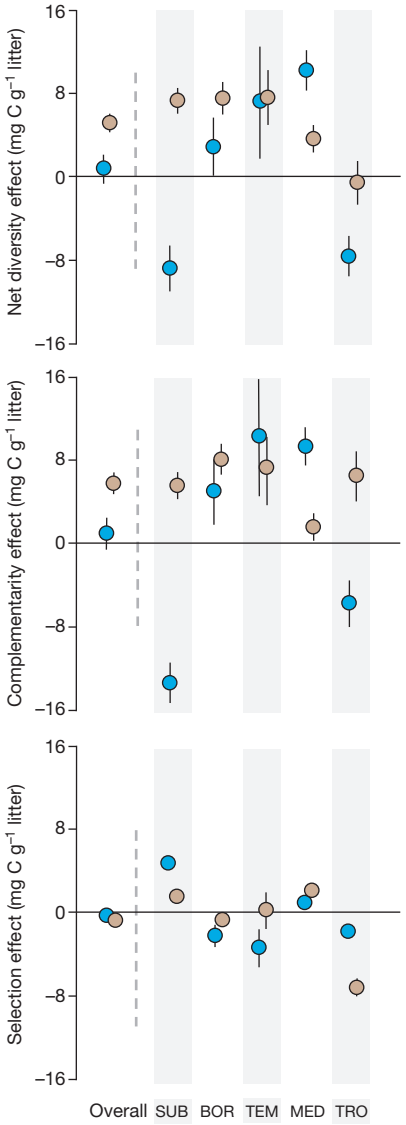

Figure 1 | Net diversity, complementarity and selection effects of plant litter mixtures on C loss. The net diversity effect is the deviation from the expected mean based on C loss measured from litter consisting of single species. The blue and brown circles show the mean effects (±s.e.m.) on C loss from litter mixtures in forest streams and on forest floors, respectively, in subarctic (SUB), boreal (BOR), temperate (TEM), Mediterranean (MED) and tropical (TRO) locations. Each circle to the right of the dashed lines shows the mean effect per ecosystem type (that is, aquatic versus terrestrial), as calculated across the three types of decomposer community ($n = 165$ litter mixtures per location and ecosystem type; see Extended Data Table 3 for statistical analyses). The circles to the left of the dashed lines show the overall mean across all locations.

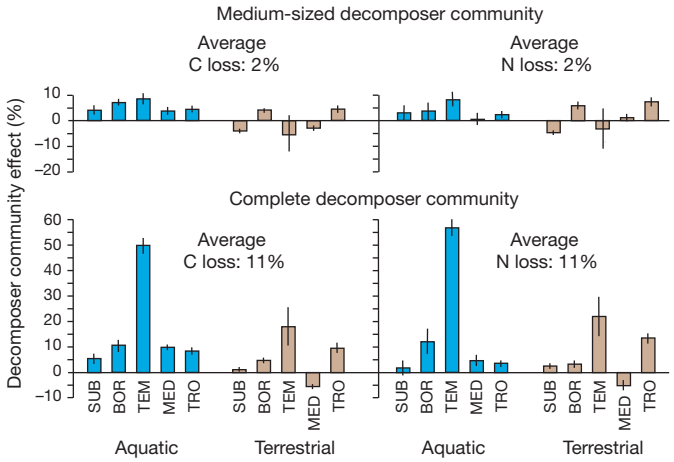

Figure 2 | Effect of decomposer community completeness on litter C and N loss. C loss (left) and N loss (right) from all litter treatments (all single species and all mixtures) exposed to medium-sized decomposers (top; percentage difference compared with the smallest mesh size) and the complete decomposer community (bottom; percentage difference compared with the smallest mesh size). The blue and brown bars show mean effects (±s.e.m.) in forest streams and on forest floors, respectively, in the five indicated locations ($n = 45$ litter treatments per location per ecosystem type; see Table 1 for statistical analyses).

the observed negative complementarity effects in subarctic and tropical streams could reflect a low density and low taxon richness of litter consumers (Extended Data Table 4) and thus limited potential for complementary resource use[21].

Our experiments also show that completeness of the decomposer community, which is rarely considered in large-scale studies, is important for C and N dynamics during litter decomposition (Fig. 2, Table 1 and Extended Data Table 5). The presence of medium-sized invertebrates (≤1 mm in diameter) in the decomposer community increased the average C and N loss across all sites by 2.1 ± 0.8% and 2.0 ± 1.0%, respectively. The complete decomposer community (which included organisms up to 5 mm in diameter) increased the average C loss across all sites by 10.6 ± 1.0% and the average N loss across all sites by 11.1 ± 1.2% (Fig. 2). This effect was consistently positive across all but the Mediterranean terrestrial site. Thus, the presence of large fauna clearly has a major impact on decomposition (Table 1), as reported previously[22–24]; however, in line with previous studies, the importance of large fauna varies among locations in aquatic[22] and terrestrial ecosystems[23,24]. In our study, the strong effects of the complete decomposer community at the temperate and tropical locations correspond to high relative abundances of millipedes and termites at the terrestrial temperate and tropical sites, respectively (Extended Data Table 6). Similarly, the large effect of the complete decomposer community at the temperate aquatic site corresponds to the high abundance of a particularly efficient amphipod detritivore (Extended Data Table 4). Our data clearly indicate that the large-bodied organisms are the most critical for decomposition. These animals also tend to face the greatest extinction risk[17].

Litter mixing and completeness of the decomposer community interacted with each other to affect C and N loss, although this interaction explains less of the variance than the main effects (Table 1). C loss and, even more so, N loss increased in the presence of particular plant functional types and with increasing completeness of the decomposer community (Table 1 and Extended Data Table 7). Although the type of decomposer community did not significantly change the net effect of diversity on C loss ($P = 0.67$) or N loss ($P = 0.30$) (Extended Data Table 3), it emerged as a significant factor in the selection effect for both C loss ($P < 0.05$) and N loss ($P < 0.05$). Additionally, the interaction between the rapidly decomposing litter type and the decomposer community was significant in explaining the selection effect and the overall net diversity effect on C loss ($P < 0.05$) and N loss ($P < 0.05$), suggesting that large decomposers are particularly important drivers of C and N loss from litter mixtures that contain rapidly decomposing litter. The food preference behaviour of decomposers could be important in accounting for this result, as has previously been implied for terrestrial[25] and aquatic[26] ecosystems.

A key result of our large-scale study is that the effects of litter diversity on C and N dynamics can be largely explained by the presence of particular functional plant types in litter mixtures, supporting the idea that the range and relative abundance of plant traits in ecosystems underlie the effects of species richness on ecosystem processes[27,28]. The effects of the presence of litter from particular plant functional types, or the interactions among these, were consistent across locations at both terrestrial and aquatic sites, together accounting for about 10% of the total variance as shown in the full analysis of variance model (Table 1, $P < 0.05$;

Table 1 | Variance in C and N loss associated with diversity and sites

Factor		C loss			N loss		
	DF	%SS	*F*	*P*	%SS	*F*	*P*
Variation associated with diversity							
Litter community: litter richness*	1	0	0	0.93	1.0	63.7	***
Litter community: remaining variation associated with FT composition†	13	10.1	66.0	***	8.9	44.4	***
Decomposer community (small, medium-sized or complete)	2	5.8	247	***	4.4	142	***
Litter community × decomposer community	28	0.8	2.45	***	1.3	3.1	***
Variation associated with sites							
Location (tropical, Mediterranean, temperate, boreal or subarctic)	4	12.1	52.8	***	16.9	66.5	***
Ecosystem (aquatic stream or terrestrial forest floor)	1	6.4	113	***	1.4	22.3	***
Location × ecosystem	4	6.3	27.7	***	8.0	31.6	***
Block (within location × ecosystem)	40	2.3	4.87	***	2.5	4.13	***
Variation associated with diversity or sites							
Decomposer community × location	8	8.6	92.1	***	7.5	61.3	***
Remaining variance	388	27.1	5.95	***	21.4	3.60	***
Total variance explained by the model	489	79.5	13.9	***	73.3	9.76	***
Residuals	1,739	20.4	–	–	26.7	–	–
Total	2,228	100.0	–	–	100.0	–	–

The relative contributions of variance in C and N loss associated with diversity and sites (expressed in percentage sums of squares (% SS)) in a large-scale leaf litter decomposition experiment. The main factors are italicized. ***, $P < 0.001$, analysis of variance based on sequential sums of squares (see Methods). See Extended Data Table 5 for details. DF, degrees of freedom; FT, functional type.
* Plant species (trees or shrubs) were selected to represent the same four functional types at each location (N-fixing, evergreen, rapidly decomposing deciduous and slowly decomposing deciduous). Linear functional type richness was fitted before litter functional type compositions.
† An alternative model omitting richness and testing in detail the litter functional type compositions in a full factorial analysis with contrasts for functional type presence/absence and interactions is presented in Extended Data Table 7. That model highlights the importance of the interaction between the litter of the N-fixing functional type and the rapidly decomposing functional type, hinting at a N-transfer mechanism.

Extended Data Table 7). Beyond the presence or absence of particular plant functional types, we found no significant effect of the richness of plant functional types in the litter on C loss ($P = 0.93$), although a positive effect was observed on N loss ($P < 0.001$) (Table 1). The effect on N loss was strongest when the most complete decomposer communities had access to the litter (litter richness × decomposer community interaction; $P < 0.05$). Our results indicate that partitioning the diversity effects into the separate contributions of the presence or absence of particular plant functional types in litter and their interactions can help move interpretations of biodiversity–ecosystem functioning experiments beyond the current dichotomy between broad generalizations and claims of idiosyncratic compositional effects[5,14,15].

An intriguing finding in this context is that the strongest positive interaction emerged between two particular litter functional types: N-fixing plants and rapidly decomposing deciduous plants (Extended Data Table 7). When these types were present together in litter mixtures, the average C loss was 13.5% greater than the average C loss of all litter combinations, and the N loss was 32.5% greater. This general pattern holds across terrestrial and aquatic ecosystems from the subarctic to the tropics. Moreover, relative to the total amount of N in the litter initially, less N remained in the litter of N-fixing plants when rapidly decomposing litter was present than when it decomposed alone (Fig. 3 and Extended Data Table 8). The rapidly decomposing litter, in turn, contained more N when litter from N-fixing plants was present than when it decomposed alone (Fig. 3 and Extended Data Table 8). On average across all of the sites, the litter of N-fixing plants lost 20.6% of its initial N when it decomposed alone but 25.0% when it decomposed in the presence of litter from rapidly decomposing plants. By contrast, the litter of rapidly decomposing plants lost 18.1% of its N when it decomposed alone but 13.4% when litter from N-fixing plants was present. This striking pattern across locations and ecosystems suggests, for the first time from field data, that N can be transferred between litter types. A plausible mechanism for this effect is that fungal decomposers tap the nutrient reservoir of the N-fixing plant litter, boosting C use and fungal growth in the N-deficient litter, which provide high-quality C[29] (see section Extended discussion on litter N transfer in Methods). The average net differences in N fluxes between single-species litter and litter mixtures of these two plant functional types account for approximately 0.25 g N per square metre of ground area, representing up to one-tenth of the total annual N input from leaf litter fall. Thus, although the biodiversity effects that we report here, in line with recent syntheses[9–11], are smaller than those noted for other ecosystem processes such as plant biomass production, these changes in N fluxes can have important consequences for the ecosystem. Even slight differences in the N dynamics in litter mixtures compared with the respective single-species litter can substantially change the N supply to primary producers and other organisms over large spatial and temporal scales[30].

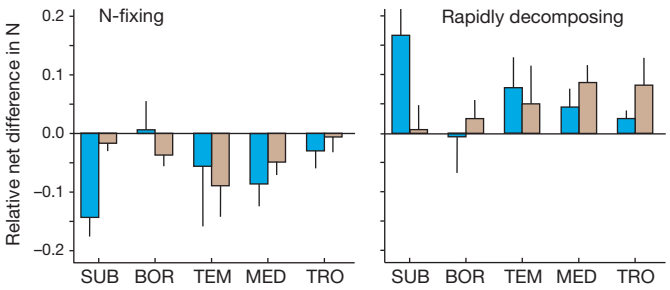

Figure 3 | Relative change in the total amount of litter N. The relative net difference between two-species mixtures (containing litter from the N-fixing and the rapidly decomposing plants) and monocultures of N-fixing plant litter (left) or rapidly decomposing plant litter (right) is shown (mean ± s.e.m., $n = 15$; see Extended Data Table 8 for statistical analyses) for litter decomposing in terrestrial (brown) and aquatic (blue) ecosystems at five locations. The relative net difference was calculated as $[(N_{i,m} - N_{f,m})/N_{i,m}] - [(N_{i,a} - N_{f,a})/N_{f,a}]$, where $N_{i,m}$ and $N_{i,a}$ are the initial (i), and $N_{f,m}$ and $N_{f,a}$ are the final (f), amounts of N in a particular litter type in a mixture (m) or alone (a).

The implications of our results are that changes in C and N cycling in response to biodiversity loss are largely predictable across vastly different latitudes in both terrestrial and aquatic ecosystems, by taking into account relatively simple plant traits and the structural characteristics of decomposer communities. To provide robust projections of how ecosystems respond to a loss of biodiversity, it is essential to identify the mechanisms that result from specific interactions between the components of biodiversity as we describe here. With the consistent patterns and mechanisms of biodiversity effects that we have shown, such projections now seem to be within reach.

METHODS SUMMARY

The field experiments followed an identical protocol at ten sites, encompassing both aquatic (forest stream) and terrestrial (forest floor) ecosystems at five locations across a latitudinal gradient spanning from the subarctic to the tropics, with intermediate locations in boreal, temperate and Mediterranean climates (Extended Data Table 1). Leaf litter from native tree or shrub species representing four common functional types (evergreen, deciduous with slowly decomposing litter, deciduous with rapidly decomposing litter, and N-fixing) that naturally occur across all locations (18 species in total; Extended Data Table 2) was exposed to decomposers in a total of 2,250 experimental microcosms set up in the field with all possible location-specific single-species and multi-species combinations. We used a randomized block design with five blocks per site. Each block contained 1 replicate of 15 combinations of litter types (that is, all possible combinations of 4 litter species) × 3 microcosm mesh sizes (totalling 45 microcosms per block). The three mesh sizes used to construct the field microcosms allowed us to establish three increasingly complete decomposer communities (small, medium-sized and complete) in the microcosms. Small-sized decomposer communities included microorganisms and fauna that passed through 50-μm and 250-μm mesh screens (DIATEX) in terrestrial and aquatic ecosystems, respectively. The medium-sized decomposer communities contained all organisms (including invertebrates) that passed through 1-mm mesh screens, whereas the complete decomposer communities included all organisms that passed through 5-mm mesh screens. Litter mass loss was allowed to proceed to the same defined decomposition stage (40–50% of the mass of the least recalcitrant litter type remaining at each location; Extended Data Table 9) to ensure the comparisons of C and N loss, as well as the effects of diversity, at a similar decomposition stage among sites, using analysis of variance models (see Methods section).

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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METHODS

Experimental design. Our field experiments followed an identical protocol at a total of ten sites, representing either an aquatic ecosystem (forest stream) or a terrestrial ecosystem (forest floor). Five locations were selected across a broad latitudinal gradient spanning from the subarctic to the tropics, with intermediate locations in boreal, temperate and Mediterranean climates (Extended Data Table 1). Across all five locations, and in both the stream and forest ecosystems, the experiments consisted of a randomized block design in which the leaf litter from 4 common native plants (corresponding to the functional types shown in Extended Data Table 2) and 11 mixtures of these litter types (corresponding to all possible litter combinations within a location) were enclosed in nylon mesh screens (DIATEX) and placed in the field in five blocks ($n = 5$ locations $\times$ 2 ecosystem types $\times$ 15 litter combinations $\times$ 3 mesh sizes $\times$ 5 blocks = 2,250 microcosms). The four functional plant types represent distinct plant C allocation strategies (deciduous versus evergreen), N acquisition strategies (N fixer versus not a N fixer) and litter recalcitrance of deciduous non-N-fixers (rapidly decomposing versus slowly decomposing).

The three mesh sizes used to construct the microcosms enabled us to distinguish three increasingly complete decomposer communities (small, medium-sized and complete) that established themselves on the decomposing litter. Small decomposers included microorganisms and small-sized fauna that passed through 50-µm and 250-µm mesh screens in terrestrial and aquatic systems, respectively. The medium-sized decomposer communities contained all organisms (including invertebrates) that passed through 1-mm mesh screens, whereas the complete decomposer communities included all decomposers that passed through 5-mm mesh screens. Litter mass loss was allowed to proceed to the same defined decomposition stage (40–50% of the litter mass of the least recalcitrant litter type remaining at each site; Extended Data Table 9) to ensure meaningful comparisons of C and N loss among all sites. At all ten sites, extra microcosms containing the fastest decomposing litter type served as benchmark indicators of decomposition rates.

Site characterization. The five stream locations were characterized in terms of their geomorphological, physical and chemical features (Extended Data Table 1). Water samples were collected for chemical analyses at the time of establishing the experiments. Samples for inorganic N and phosphorus determination were filtered over 0.45-µm pore-size cellulose acetate membrane filters and transported to the laboratory in a cooler at about 5 °C, where they were frozen for later analysis at Eawag, Switzerland.

At the five forest sites (Extended Data Table 1), the leaf area index was measured at breast height on a uniformly cloud-covered day when the forest canopy was fully developed, using an LAI-2000 Plant Canopy Analyzer (LI-COR) for the subarctic location, an LAI-2200 Plant Canopy Analyzer (LI-COR) for the Mediterranean and tropical locations, and a SunScan Canopy Analysis System (Delta T Devices) for the temperate locations. Data for the boreal location were provided by K. Bishop & P.-E. Mellander. To characterize the soil at each of the terrestrial sites, three samples from each experimental block were taken with a soil corer (5 cm diameter, 10 cm height), pooled, stored in plastic bags at 4 °C, then sent cooled to the University of Göttingen (Germany). Sieved soil samples (<2 mm sieve pore size) were analysed for pH (2 g soil in 20 ml 0.01 M $CaCl_2$) and C and N concentration (using an NA 1500 Carlo Erba elemental analyser). The microbial biomass of the soil was estimated using the substrate-induced respiration (SIR) method. The microbial respiratory response was measured in an electrolytic O_2-microcompensation apparatus at 22 °C. These measurements were made hourly for 24 h. The microbial biomass was measured after the addition of glucose (8 mg C g^{-1} dry soil) as a substrate to saturate the catabolic activity of the microorganisms. The maximum initial respiratory response (MIRR; µl O_2 g^{-1} dry mass h^{-1}) was calculated as the mean of the lowest three readings within the first 10 h, and the microbial biomass was calculated as $C_{mic} = 38 \times$ MIRR (in µg C_{mic} g^{-1} soil dry mass).

Data loggers (SL52T, Signatrol) were installed in some microcosms at all ten sites, to record the temperature every 2 h. These temperature measurements were taken in the same litter treatment for all three mesh sizes in three of the five experimental blocks.

Leaf litter collection. A total of 20 litter types were collected at the 5 locations of our coordinated experiment. This litter corresponded to the same four functional types per location that were introduced above: N-fixing plants, rapidly decomposing deciduous plants, slowly decomposing deciduous plants and evergreen plants (Extended Data Table 2). Litter from these four functional types varies with respect to several quality traits[31] (Extended Data Table 2). The selected species were common native trees or, in two cases, native woody shrubs (*Vaccinium vitis-idaea* and *Rhododendron tomentosum*) occurring at each location. The litter was collected during location-specific leaf senescence either by hand (*V. vitis-idaea* and *R. tomentosum*) or by using litter traps. An exception was litter from the temperate evergreen species *Ilex aquifolium*, which was obtained by cutting branches in the field and simulating senescence in the laboratory for three weeks. Leaves with signs of herbivory or disease were discarded. The litter from multiple individual trees or shrubs of each species was pooled and dried at 40 °C.

Leaf litter field incubations. Stream experiments were conducted by exposing 5 g litter batches in tetrahedral mesh microcosms (17 cm $\times$ 25 cm) made of one of three mesh sizes (250 µm, 1 mm or 5 mm) to provide access to decomposer communities differing in body size. The microcosms were randomly attached (about 40 cm distance between microcosms) to five 20-m metal chains, each in a separate riffle (short, relatively shallow sections of streams with non-stagnating water) 20 m or farther apart from each other (experimental blocks). The chains were fixed in the stream with reinforcing bars in fairly homogeneous sand–gravel stream sections, where leaves accumulated naturally. All microcosms were submerged at depths sufficient to ensure that they were not exposed to air when water levels dropped. Care was taken to expose the litter to constant flow conditions, avoiding deep depositional areas (that is, pools and backwaters) with slow or no flow and rocky riffles with broken flow.

Terrestrial experiments on the forest floor were conducted by incubating 8 g location-specific litter (4 g only in the subarctic because of limited litter availability for some species) in field microcosms made of polyethylene cylinders (15 cm diameter, 10 cm height) covered with 50-µm mesh at the top and bottom to allow the passage of water but to prevent the entry of natural litter fall from above and the loss of small litter particles from the bottom. Two windows (5 cm $\times$ 18 cm) were cut into the cylinders and covered with 50-µm, 1-mm or 5-mm mesh to provide access to decomposer communities differing in body size. The windows were cut close to the bottom of the cylinders to ensure that decomposers had access to a continuous layer of litter outside and inside the microcosms. An additional 1.5-cm height plastic ring of the same diameter as the cylindrical microcosms was attached at the bottom of the microcosm, making it possible to push the microcosms gently into the top soil (to a depth of 1.5 cm). This ring held the terrestrial microcosms properly in place while the bottom mesh was in intimate contact with the soil surface. In cases in which pushing the microcosms into the soil was difficult (for example, in the tropical forest with its dense superficial tree roots), the 1.5-cm rings were fitted with a separate plastic or metal ring before placing the microcosms. The microcosms were separated from each other by at least 50 cm. They were randomly distributed within blocks that were established at least 20 m apart from each other.

Sample harvest and processing. We removed the decomposing litter of all species from the field when 40–50% of the initial litter mass of the fastest decomposing species was remaining. As a consequence, the duration of litter decomposition varied among locations and ecosystem types (Extended Data Table 9). This procedure ensured that similar decomposition stages were sampled at all sites, facilitating meaningful comparisons of decomposition rates and litter diversity effects. All litter samples were separated into the constituent species immediately after litter retrieval. The litter recovered from the streams was gently washed to remove any adhering material and invertebrates. The litter from the terrestrial sites was cleaned by gently brushing off any dirt without using water, to prevent the leaching of nutrients. The litter samples were then dried at 65 °C for 48 h. A correction factor was used to convert the initial litter mass (weighed after drying at 40 °C) to the final dry mass, based on ten randomly selected samples per litter type that were successively dried and weighed in the laboratory first at 40 °C and then at 65 °C.

Litter C and N loss. The initial C and N concentrations of each of the 20 individual litter types were determined from 5 random samples. The final C and N concentrations after retrieval of the litter from the field were also measured for each individually sorted litter type from each microcosm. This process resulted in a total of 5,400 samples for which to calculate the percentage C and N loss for each litter type under the various conditions. Following the determination of litter dry mass, all initial and final samples were ground with a ball mill (Retsch PM 400) to a fine homogeneous powder. Subsamples of 3 mg were analysed for C and N concentrations using a CHN elemental analyser (Flash EA 1112 Series, Thermo Finnigan). C and N loss (%) from the litter during field exposure was calculated as $100 \times [(M_i \times CN_i) - (M_f \times CN_f)] / (M_i \times CN_i)$, where M_i and M_f are the initial and final litter dry mass, respectively, and CN_i and CN_f are the initial and final C or N concentration (% of litter dry mass). Using C loss (%) rather than total litter mass loss allowed us to correct for any possible inorganic contamination of the litter retrieved from the field.

Analyses of diversity effects and statistical models. The net diversity effects, comprising complementarity and selection effects, on both C and N loss were calculated in species mixtures[20]. The net diversity effect was calculated as the sum of the complementarity and selection effects and contrasts the actual C and N loss observed for mixtures of plant functional types with that expected based on the C and N loss measured in single-species treatments. The net diversity effect represents the sum of synergistic or antagonistic interactions (that is, complementarity effects) and those due to the presence of a dominant species (that is, selection effects). Data were square-root transformed (keeping the original negative and positive signs

for the transformed values) to meet the assumptions for the analysis of variance of net diversity, complementarity and selection effects (see details below).

Analysis of variance models based on sequential sums of squares (type I) were used to assess the effects of diversity (the richness of plant litter functional types or the presence or absence of a given functional type and its interaction with other functional types), the completeness of the decomposer community (small, medium and large (complete)), the location across the latitudinal gradient and the ecosystem type (terrestrial versus aquatic) on percentage C and N loss. To ensure meaningful comparisons across the locations, several standardization methods were tested to remove any variation associated with the differences in incubation length. These methods included standardizing relative to the following: 1) a standard litter type from a non-native plant, *Ailanthus altissima*, that decomposed at all locations during the experiments; 2) the overall mean C or N loss per mesh size across locations; and 3) the mean C or N loss per mesh size of the rapidly decomposing functional type across locations. Because the results were consistent irrespective of standardization, the final model is presented using the non-standardized data.

The model terms were fitted to account for the dependency between the richness of plant litter functional types and the functional type composition (the presence or absence of a given functional type and interactions between functional types). First, functional type composition was partitioned into a contrast for richness and residual functional type composition (Table 1 and Extended Data Table 5). Second, as shown in Extended Data Table 7, we omitted the richness term and instead resolved the functional type composition into a full factorial analysis with contrasts for functional type presence or absence and interactions. In this model, the decomposer community was fitted as a log–linear contrast (small to large mesh size was expressed as the logarithm of the mesh size of the microcosms, which produced a linear relationship of the three mesh sizes). We also removed all of the other non-significant interaction terms in multiple successive model-fitting steps. These two alternative analyses reflect different partitionings of the functional type composition term into contrasts; they allowed us to compare the explanatory power of the richness contrast with the presence/absence contrast. A perfect linear richness effect would be found if all presence/absence contrasts had equal coefficients and did not interact. In this case, the mean squares or the richness effect with only one degree of freedom would be much larger than that of the combined mean squares of the presence/absence main effects of the four litter types with four degrees of freedom. In both models, the terms 'location' and 'ecosystem type' were tested at the block level. All other terms were tested against the residuals.

A similar analysis of variance approach was used to test independently for the effects of these same factors on complementarity and selection effects, as well as on net diversity effects (Extended Data Table 3). In a separate analysis of variance (Extended Data Table 8), we also tested whether the net loss of the total amount of N relative to the initial amount of N differed when litter of particular plant functional types (for example, rapidly decomposing litter and litter of N-fixing plants) decomposed together as opposed to decomposing separately, which we interpreted as an indication of N transfer between litter species. The location and ecosystem type were also included in this analysis. All statistical analyses were performed with R software version 2.8.0.

Extended discussion on litter N transfer. Although our data suggest that N was transferred from the litter of N-fixing plants to rapidly decomposing litter, alternative mechanisms cannot be entirely ruled out. In particular, N incorporated into decomposing litter can originate not only from another co-occurring litter type but also from the N pool in the soil or stream water or from microbial N fixation[32]. However, N transfer from such alternative N sources does not readily explain the concomitant reciprocal changes that we observed between the litter of N-fixing plants and rapidly decomposing litter. Moreover, the idea that N transfer occurred between the two litter types is further supported by a positive net diversity effect on C loss that we observed only when these two particular litter functional types were both present (Extended Data Table 3). Additional support for our interpretation comes from ^{15}N tracer studies in microcosms with tropical[28] and temperate[33] forest litter, which are proof of principle that active biological transfer of N through microorganisms, particularly saprotrophic fungi, can occur. Our large-scale field experiment suggests that this phenomenon might be widespread across terrestrial and aquatic ecosystems and across a wide variety of forest types and climatic conditions.

It had been proposed that N transfer is driven by a gradient in N concentration between litter types[4,5], the rationale being that the element that limits the decomposition rate is N. However, the scenario now unfolding from our experiment (Fig. 3) and the recent isotope tracer studies under laboratory conditions[28,33] is that N transfer is stoichiometrically controlled. The crucial determinant that defines the gradient along which N will be transferred in litter mixtures seems to be the demand for N relative to the availability of C (and possibly that of other elements critical for decomposer growth), rather than differences in the N concentration. A litter with high C quality favours rapid microbial growth, which in turn entails a high demand for N (and other nutrients), resulting in N acquisition from neighbouring nutrient pools. In extreme cases, the N source litter may even have a lower N concentration than the N sink litter[33], provided that the C quality of both litter types is sufficiently different. In accordance with this mechanism, the decomposition of recalcitrant litter types in our study (slowly decomposing and evergreen plant functional types) was not accelerated by the presence of litter from N-fixing plant species (Extended Data Table 7), although those recalcitrant litter types had similarly low or lower initial N concentrations than the rapidly decomposing litter species, which consistently benefited from the presence of N-fixing plant litter.

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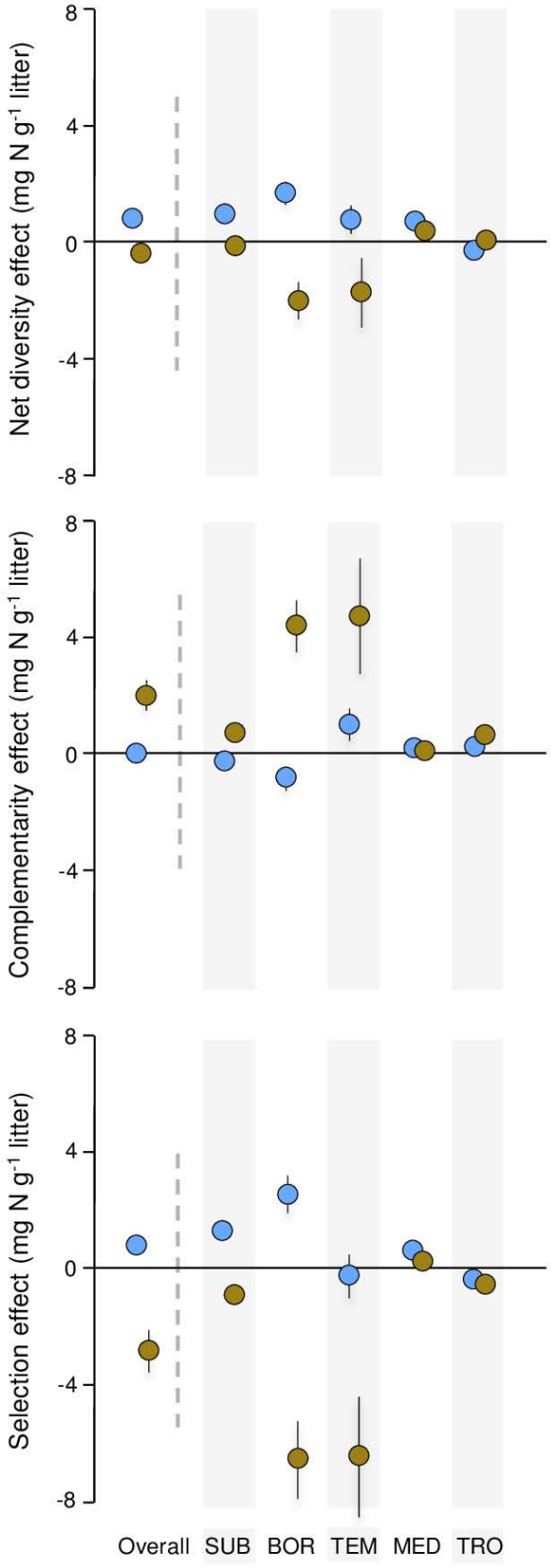

Extended Data Figure 1 | Net diversity, complementarity and selection effects of plant litter mixtures on N loss. The net diversity effect is the deviation from the expected mean based on N loss measured from litter consisting of single species. The blue and brown circles show the mean effects (±s.e.m.) on N loss from litter mixtures in forest streams and on forest floors, respectively, in subarctic (SUB), boreal (BOR), temperate (TEM), Mediterranean (MED) and tropical (TRO) locations. Each circle to the right of the dashed lines shows the mean effect per ecosystem type (that is, aquatic versus terrestrial), as calculated across the three types of decomposer communities (n = 165 litter mixtures per location and ecosystem type; see Extended Data Table 3 for statistical analyses). The circles to the left of the dashed lines show the overall mean across all locations (n = 825 litter mixtures per ecosystem type).

Extended Data Table 1 | Characteristics of aquatic and terrestrial ecosystems at five widely dispersed locations

Aquatic Locations	**Subarctic**	**Boreal**	**Temperate**	**Mediterranean**	**Tropical**
Site	Kopperåsen Sweden	Krycklan Sweden	Mosbeek The Netherlands	Maureillas France	Petit Saut French Guiana
Coordinates	68°26' N, 18°28'E	64°16' N, 19°50' E	52°26' N, 5°32' E	42°28' N, 2°48' E	5°04' N, 53°00' W
Dominant riparian tree cover	*Salix* spp., *Sorbus aucuparia*	*Picea abies*, *Betula pubescens* *Alnus incana*	*Fagus sylvatica*	*Quercus ilex*, *Corylus avellana*, *Alnus glutinosa*	~140 different canopy species
Altitude (m a.s.l.)	445	200	37	180	35
Catchment (km^2)	1.1	19.2	4.9	18.5	0.6
Distance to source (km)	1.6	4.0	1.3	8.8	1.0
Stream order	1	3	2	3	2
Slope (%)	12.7	2	0.7	2.3	2
Mean channel width (m)	2.5	4.6	2.5	4.5	2.6
Mean depth (m)	0.12	0.38	0.19	0.19	0.20
MAT (°C)*	0.9	1.8	10.2	15.4	25.4
M Jan T (°C)*	-9.7	-10.0	3.6	8.3	24.9
M July T (°C)*	12.3	15.2	17.4	23.9	25.2
MAP (mm)*	352	643	814	766	2519
Mean stream temperature during experiment (°C)	6.4	4.6	7.2	5.7	24.4
Temperature range during experiment (°C)	0.6-14.2	0.1-9.9	5.5-9.3	1.9-11.3	23.5-25.4
Conductivity (µS/cm)	122	19	233	190	19
pH	7.3	7.1	6.8	7.9	7.7
Dissolved oxygen (mg/L)	9.3	11.0	11.3	11.4	n.d.
Alkalinity (mmol/L)	0.78	0.55	0.33	1.33	0.23
N-NO_3^- (mg/L)	0.02	0.27	7.45	0.18	<0.02
N-NH_4^+ (µg/L)	n.d.	<20	154	20	<5
SRP† (µg/L)	<2	18	16	18	<1
Terrestrial Locations	**Subarctic**	**Boreal**	**Temperate**	**Mediterranean**	**Tropical**
Site	Abisko, Sweden	Krycklan, Sweden	Leuvenemse Bos, The Netherlands	Barroubio, France	Paracou, French Guiana
Coordinates	68°21' N, 18°49' E	64°14' N, 19°50' E	52°18' N, 5°41' E	43°23' N, 2°51' E	5°18' N, 52°55' W
Dominant tree cover	*Betula pubescens*	*Betula pubescens*, *Picea abies*	*Fagus sylvatica*	*Quercus ilex*, *Fraxinus angustifolia*	~140 different canopy species
Leaf area index (LAI)	1.71 ± 0.15 (tree) 3.28 ± 0.29 (shrub)	6.5‡	3.85 ± 0.12	3.66 ± 0.02	5.72 ± 0.25
MAT (°C)*	0.9	1.8	10.7	14.6	25.4
M Jan T (°C)*	-9.7	-10.0	4.3	7.4	24.9
M July T (°C)*	12.3	15.2	18.0	23.3	25.2
MAP (mm)*	352	643	911	670	2519
Soil pH	4.63 ± 0.27	4.70 ± 0.12	3.29 ± 0.06	6.56 ± 0.23	4.80 ± 0.04
Soil C_{mic} (µg g^{-1})§	4602 ± 2870	1266 ± 589	2937 ± 820	439 ± 87	648 ± 37
Soil C (%)§	27.36 ± 0.60	3.63 ± 0.06	25.21 ± 1.03	4.57 ± 0.72	2.84 ± 0.30
Soil N (%)§	0.95 ± 0.01	0.19 ± 0.00	1.14 ± 0.03	0.39 ± 0.04	0.19 ± 0.01

* Means were calculated based on 10-year records between 1998 and 2008 from the closest possible meteorological station.
† Soluble reactive phosphorus ≈ ortho-phosphate.
‡ Data courtesy of K. Bishop and P.-E. Mellander.
§ Soil microbial biomass (C_{mic}), soil C and soil N are expressed on a dry mass basis.

Extended Data Table 2 | Plant functional types, species identity and litter quality traits

	Plant Functional Type			
Location	**N-fixing**	**Deciduous, Rapidly decomposing**	**Deciduous, Slow- decomposing**	**Evergreen**
Subarctic	*Alnus incana* (L.) Moench	*Sorbus aucuparia* L.	*Populus tremula* L.	*Vaccinium vitis-idaea* L.
Boreal	*Alnus incana* (L.) Moench	*Prunus padus* L.	*Betula pubescens* Ehrh.	*Rhododendron tomentosum* Harmaja
Temperate	*Alnus glutinosa* (L.) Gaertn.	*Salix cinerea* L.	*Fagus sylvatica* L.	*Ilex aquifolium* L.
Mediterranean	*Alnus glutinosa* (L.) Gaertn.	*Fraxinus angustifolia* Vahl	*Pistacia terebinthus* L.	*Quercus ilex* L.
Tropical	*Diplotropis purpurea* (Rich.) Amshoff	*Qualea rosea* Aubl.	*Vochysia densiflora* Spruce ex Warm	*Eperua falcata* Aubl.
Quality trait*				
N	2.15 ± 0.28	0.97 ± 0.11	0.73 ± 0.10	1.05 ± 0.18
Lignin	17.2 ± 3.6	12.0 ± 2.9	16.5 ± 2.5	22.4 ± 4.1
Water saturation	238 ± 37	332 ± 182	222 ± 114	123 ± 28
Condensed tannins	1.48 ± 0.84	1.76 ± 0.54	2.68 ± 0.44	1.58 ± 0.35

Leaf litter was sampled from location-specific native tree species corresponding to four functional types (top) varying in quality traits associated with decomposition (bottom).
* All data are shown as percentage dry mass (mean ± s.e.m., $n = 5$). Methods are described in detail in ref. 31.

Extended Data Table 3 | Results of analyses of variance testing for the net diversity effect (NE), complementarity effect (CE) and selection effect (SE) on C loss (top) and N loss (bottom) from decomposing leaf litter*

Source of variation	Net diversity			Complementarity			Selection		
	DF_{NE}	F_{NE}	P_{NE}	DF_{CE}	F_{CE}	P_{CE}	DF_{SE}	F_{SE}	P_{SE}
Effect on C loss									
N-fixer (NF)	1	3.53	0.06	1	0.64	0.42	1	0.06	0.80
Rapid decomposer (RD)	1	0.41	0.52	1	0.51	0.48	1	0.05	0.82
Slow decomposer (SD)	1	0.28	0.59	1	0.17	0.68	1	0.11	0.75
Evergreen (EG)	1	0.02	0.90	1	0.61	0.43	1	5.60	<0.05
NF × RD	1	5.25	<0.05	1	2.35	0.13	1	7.95	<0.01
RD × EG	1	0.63	0.43	1	0.00	0.99	1	7.64	<0.01
Decomposer comm. (DC)	2	0.40	0.67	2	1.11	0.33	2	3.29	<0.05
NF × DC	2	4.40	<0.05	2	1.99	0.14	2	2.60	0.07
RD × DC	2	5.09	<0.01	2	3.09	<0.05	2	3.59	<0.05
SD × DC	2	5.57	<0.01	2	4.43	<0.05	2	0.69	0.50
NF × SD × DC	3	0.41	0.74	3	0.28	0.83	3	5.08	<0.01
Location†	4	11.68	<0.001	4	11.08	<0.001	4	52.60	<0.001
NF × Location	4	1.98	0.10	4	4.12	<0.01	4	5.41	<0.001
RD × Location	4	3.58	<0.01	4	2.55	<0.05	4	4.11	<0.01
SD × Location	4	0.52	0.72	4	2.25	0.06	4	11.46	<0.001
EG × Location	4	1.51	0.20	4	2.17	0.07	4	13.63	<0.001
NF × RD × Location	4	1.11	0.35	4	2.15	0.07	4	3.02	<0.05
RD × EG × Location	4	1.73	0.14	4	1.67	0.15	4	3.08	<0.05
DC × Location	8	4.93	<0.001	8	4.36	<0.001	8	7.91	<0.001
NF × DC × Location	8	4.16	<0.001	8	2.28	<0.05	8	2.36	<0.05
RD × DC × Location	8	2.26	<0.05	8	1.54	0.14	8	1.57	0.13
SD × DC × Location	8	0.74	0.65	8	1.71	0.09	8	4.43	<0.001
NF × SD × DC × Location	12	0.91	0.53	12	1.12	0.34	12	3.26	<0.001
RD × SD × DC × Location	15	0.79	0.69	15	0.83	0.65	15	1.97	<0.05
Ecosystem type (ET)†	1	10.9	<0.001	1	15.8	<0.001	1	5.23	<0.05
RD × ET	1	0.45	0.50	1	0.57	0.45	1	22.17	<0.001
SD × ET	1	5.71	<0.05	1	1.99	0.16	1	5.42	<0.05
EG × ET	1	1.70	0.19	1	5.17	<0.05	1	9.74	<0.01
RD × SD × ET	1	0.89	0.35	1	1.52	0.22	1	5.42	<0.05
ET × Location†	4	11.12	<0.001	4	15.29	<0.001	4	8.58	<0.001
DC × ET	2	1.18	0.31	2	1.92	0.15	2	4.59	<0.05
DC × Location × ET	8	4.02	<0.001	8	4.30	<0.001	8	5.81	<0.001
NF × DC × Location × ET	15	2.09	<0.01	15	1.53	0.09	15	0.98	0.46
RD × DC × Location × ET	14	1.36	0.16	14	1.30	0.20	14	1.90	<0.05
Block	40	5.43	<0.001	40	5.38	<0.001	40	2.10	<0.001
Residuals	1437			1437			1437		
Effect on N loss									
N-fixer (NF)	1	0.63	0.43	1	0.02	0.88	1	0.22	0.63
Rapid decomposer (RD)	1	2.97	0.09	1	0.59	0.44	1	3.52	0.06
Slow decomposer (SD)	1	12.62	<0.001	1	7.93	<0.01	1	16.20	<0.001
Evergreen (EG)	1	0.04	0.83	1	1.44	0.23	1	1.27	0.26
SD × EG	1	0.20	0.65	1	8.67	<0.01	1	3.78	<0.05
Decomposer comm. (DC)	2	1.22	0.30	2	5.75	<0.01	2	3.39	<0.05
NF × DC	2	1.30	0.27	2	4.27	<0.05	2	0.76	0.47
RD × DC	2	4.23	<0.05	2	9.06	<0.001	2	5.90	<0.01
SD × DC	2	25.25	<0.001	2	11.72	<0.001	2	23.30	<0.001
Location†	4	6.28	<0.001	4	5.32	<0.001	4	7.01	<0.001
NF × Location	4	5.33	<0.001	4	0.68	0.61	4	1.93	0.10
SD × Location	4	5.87	<0.001	4	2.56	<0.01	4	5.36	<0.001
EG × Location	4	3.80	<0.01	4	1.84	0.12	4	3.22	<0.05
DC × Location	8	11.30	<0.001	8	14.03	<0.001	8	15.08	<0.001
NF × DC × Location	8	3.18	<0.01	8	3.18	<0.01	8	2.44	<0.05
RD × DC × Location	12	3.48	<0.001	12	3.68	<0.001	12	3.92	<0.001
SD × DC × Location	8	2.56	<0.01	8	6.93	<0.001	8	6.68	<0.001
Ecosystem type (ET) †	1	61.29	<0.001	1	49.46	<0.001	1	82.66	<0.001
ET × Location†	4	16.42	<0.001	4	19.68	<0.001	4	20.08	<0.001
NF × ET	1	10.46	<0.01	1	1.31	0.25	1	9.47	<0.01
NF × Location × ET	4	8.33	<0.001	4	4.12	<0.01	4	6.93	<0.001
NF × RD × ET	2	6.37	<0.01	2	2.10	0.12	2	3.89	<0.05
SD × ET	1	4.54	<0.05	1	30.09	<0.001	1	15.92	<0.001
SD × Location × ET	4	10.69	<0.001	4	17.78	<0.001	4	17.21	<0.001
NF × SD × Location × ET	10	2.19	<0.05	10	5.03	<0.001	10	5.21	<0.001
EG × Location × ET	5	2.75	<0.05	5	3.42	<0.01	5	2.40	<0.05
DC × ET	2	15.11	<0.001	2	21.04	<0.001	2	19.83	<0.001
RD × DC × ET	2	0.17	0.85	2	7.70	<0.001	2	3.63	<0.05
DC × Location × ET	8	5.96	<0.001	8	7.90	<0.001	8	6.70	<0.001
NF × DC × Location × ET	10	2.81	<0.01	10	1.59	0.11	10	1.01	0.43
SD × DC × ET	2	5.26	<0.01	2	8.19	<0.001	2	9.11	<0.001
SD × DC × Location × ET	8	4.17	<0.001	8	4.52	<0.001	8	5.78	<0.001
Block	40	2.55	<0.001	40	2.44	<0.001	40	1.80	<0.01
Residuals	1460			1460			1460		

* Interaction terms omitted from the final model are not significant for any of the three response variables.
† Location, ecosystem type and their interaction were tested against the block rather than against the residual.

Extended Data Table 4 | Characteristics of stream macroinvertebrate communities at the five tested locations*

Location	Detritivores		Detritivore community composition†				Predators		
	Density (# m^{-2})	Taxon richness	Plecoptera (%)	Trichoptera (%)	*Gammarus* (%)	Dominant taxa	Density (# m^{-2})	Taxon richness	Dominant taxa
Subarctic	46.2 ±12.8	5	95.7 ±4.8	4.3 ±4.8	-	*Leuctra digitata*, *Capnopsis schilleri*	40.0 ±20.4	7	*Dicranota*, *Rhyacophila*, *Diura nanseni*
Boreal	267.3 ±258.5	8	96.8 ±1.3	3.2 ±1.2	-	*Protonemura meyeri*, *Nemoura flexuosa*, *Leuctra digitata*	46.6 ±30.7	8	*Isoperla*, *Rhyacophila nubila*
Temperate	332.3 ±62.6	13	4.3 ±5.8	10.2 ±16.1	82.3 ±13.7	*Gammarus pulex*, *Chaetopteryx villosa*, *Sericostoma personatum*	130.7 ±47.4	13	*Dugesia gonocephala*, *Plectrocnemia conspersa*
Mediterranean‡	432.1 ±330.6	10	62.9 ±26.2	36.1 ±26.6	1.0 ±2.2	Leuctridae, Taeniopterygidae, Nemouridae, Limnephilidae	418.3 ±239.1	11	Perlodidae, Athericidae, Limoniidae, Rhyacophilidae
Tropical	8.6 ±14.7	3	-	21.4 ±39.3	-	*Phylloicus*, Pyralidae, Tipulidae	12.3 ±22.8	4	Perlidae, Calopterygidae

* The mean density and total taxon richness of detritivores, their main invertebrate predators, and the mean proportion of Plecoptera, Trichoptera and *Gammarus* as a percentage of total detritivore abundance (mean ± s.d.) are shown. All samples were collected using a 500-μm mesh net at the same time of year as the main experiment (although in different years in some cases). Specific sampling protocols differed between locations, with the density standardized to the number of individuals per metre squared. For the subarctic site, six replicate kick samples were taken, each from an area of 1 m × 0.35 m for 1 min, during September 2006. Identification was mostly to the species level[34]. For the boreal site, four replicate Surber samples per year were taken for three years, during October 2010–2012, with a quadrat size of 0.25 m × 0.5 m. Identification was mostly to the species level (B.G.M. and P.-O. Hoffsten, unpublished observations). For the temperate site, five replicate sweep net samples were taken, each from an area of 0.3 m × 5 m, in October 1992. Identification was mostly to the species level[35]. For the Mediterranean site, five replicate Surber samples were taken, with a quadrat size of 0.33 m × 0.31 mm, in January 2014. Identification was mostly to the family level (E.C. and S. Lamothe, unpublished observations). For the tropical site, ten replicate natural leaf packs (fist-sized handfuls of leaves picked from the stream bed) were taken from each of seven streams in May 2007. Abundances per leaf pack were converted to densities based on standardized visual estimates of stream-bed litter cover. Identification was mostly to the family level (A.B., M. Schindler, M. S. Moretti and M.O.G., unpublished observations).

† Detritivore community composition data do not sum to 100% at all locations, owing to the presence of other dipteran (Tipulidae), lepidopteran (Pyralidae) and crustacean (Asellidae) shredders at the temperate site, and tipulid and pyralid shredders at the tropical site.

‡ The caddisfly *Micrasema* (Brachycentridae) was common at the Mediterranean site but was small and was not regarded as a shredder.

Extended Data Table 5 | Full model output of the relative contributions of variance associated with diversity and sites to explain C and N loss

Source of variation	DF	C loss			N loss		
		%SS	F	P	%SS	F	P
Variation associated with diversity							
Litter community							
Litter richness†	1	0	0.01	0.93	1.0	63.7	***
Litter diversity†	2	0.1	2.61	0.07	0.3	8.29	***
Variation associated with functional type (FT) composition‡	11	10.0	77.5	***	8.6	50.9	***
Decomposer community (DC)	2	5.8	247	***	4.4	142	***
Litter community x DC							
Richness x DC	2	0	0.37	0.69	0.1	3.45	*
Diversity x DC	4	0	0.70	0.59	0.0	0.07	0.99
FT composition x DC	22	0.8	2.96	***	1.2	3.61	***
Variation associated with sites							
Location	4	12.1	52.8	***	16.9	66.5	***
Richness x Location	4	0.1	2.07	0.08	0.3	5.06	***
Diversity x Location	8	0.2	2.35	*	0.3	2.37	*
FT compositions x Location	44	15.8	30.6	***	10.4	15.4	***
DC x Location	8	8.6	92.1	***	7.5	61.3	***
Richness x DC x Location	8	0	0.51	0.85	0.1	0.53	0.83
Diversity x DC x Location	16	0.3	1.36	0.15	0.2	0.84	0.64
FT composition x DC x Location	88	1.6	1.56	***	1.7	1.28	*
Ecosystem	1	6.4	113	***	1.4	22.3	***
Location x Ecosystem	4	6.3	27.7	***	8.0	31.6	***
Richness x Ecosystem	1	0.1	5.79	*	0	1.02	0.31
Richness x Location x Ecosystem	4	0.1	1.25	0.29	0.2	3.21	*
Diversity x Ecosystem	2	0	0.62	0.54	0	1.27	0.28
Diversity x Location x Ecosystem	8	0.2	2.37	*	0.1	1.11	0.35
FT Composition x Ecosystem	11	1.0	7.94	***	1.4	8.30	***
FT Composition x Location x Ecosystem	44	1.7	3.30	***	1.9	2.81	***
DC x Ecosystem	2	1.9	79.7	***	0.9	27.7	***
DC x Location x Ecosystem	8	2.4	25.7	***	1.9	15.9	***
Richness x DC x Ecosystem	2	0	0.36	0.70	0	0.60	0.55
Richness x DC x Location x Ecosystem	8	0.1	0.70	0.69	0	0.33	0.96
Diversity x DC x Ecosystem	4	0	0.35	0.84	0.1	1.40	0.23
Diversity x DC x Location x Ecosystem	16	0.1	0.38	0.99	0.2	0.79	0.70
FT Composition x DC x Ecosystem	22	0.3	1.14	0.30	0.4	1.08	0.36
FT Composition x DC x Location x Ecosystem	88	1.2	1.17	0.13	1.2	0.92	0.69
Block (within location x ecosystem)	40	2.3	4.87	***	2.5	4.13	***
Total variance explained by the model	489	79.6	13.9	***	73.3	9.76	***
Residuals	1739	20.4			26.7		
Total	2228	100.0			100.0		

Variance associated with diversity and sites is expressed in percentage sums of squares (% SS); levels of significance are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

† Plant species were selected to represent the same four functional types (FTs) at each location (N-fixing, evergreen, rapidly decomposing deciduous trees or shrubs, or slowly decomposing deciduous trees or shrubs). Litter FT richness (linear contrast) and litter diversity (factorial contrast) were fitted before litter FT compositions.

‡ An alternative model omitting richness and testing in detail the litter FT compositions in a full factorial analysis with contrasts for FT presence/absence and interactions is presented in Extended Data Table 7. That model highlights the importance of the interaction between the litter of the N-fixing FT and the rapidly decomposing FT, hinting at a N-transfer mechanism.

Extended Data Table 6 | Characteristics of soil fauna communities at the five tested locations*

Location	Mesofauna*						
	Microbi-detritivores		Dominant taxa‡		Predators		Dominant taxa‡
	Density (# m^{-2})	Taxon richness†	Collembola (%)	Acari (%)	Density (# m^{-2})	Taxon richness†	
Subarctic	4068 ±2254	8	46.9 ±13.0	53.1 ±13.0	506 ±209	1	Gamasida
Boreal	9824 ±3750	10	61.9 ±14.9	38.1 ±14.9	690 ±356	1	Gamasida
Temperate	17020 ±6846	11	75.0 ±8.3	25.0 ±8.3	711 ±347	2	Gamasida (73%) Diplura (27%)
Mediterranean	9222 ±6514	10	21.9 ±6.9	78.1 ±6.9	1386 ±598	2	Gamasida (64%) Diplura (36%)
Tropical	641 ±134	6	3.9 ±3.7	96.0 ±3.7	276 ±106	3	Gamasida (47%) Diplura (53%)
Location	**Macrofauna***						
	Detritivores		Dominant taxa‡		**Predators**		Dominant taxa‡
	Density (# m^{-2})	Taxon richness†			Density (# m^{-2})	Taxon richness†	
Subarctic	595 ±249	10	Diptera (68%) Gastropoda (25%)		588 ±197	9	Araneidae (41%) Diptera (35%)
Boreal	333 ±185	9	Diptera (82%) Annelida (13%)		1824 ±1674	7	Diptera (73%) Coleoptera (20%)
Temperate	81 ±59	6	Diplopoda (60%) Gastropoda (23%)		3640 ±1534	8	Chilopoda (88%)
Mediterranean	501 ±219	10	Isopoda (43%) Diptera (38%)		2244 ±2021	16	Chilopoda (51%) Hymenoptera (30%)
Tropical	1750 ± 3115	10	Isoptera (34%) Diptera (26%)		1813 ±1515	13	Hymenoptera (59%) Pseudoscorpionida (32%)

* The mean density, the total taxon richness and the proportion of dominant taxa as a percentage of total community abundance are shown (mean ± s.d.). Communities are divided into mesofauna and macrofauna, reflecting an increase in body size that relates to mesh size differences in the field microcosms.

† Taxon richness is based on the number of observed families.

‡ Dominant taxa data are based on a lower taxonomic resolution than taxon richness, mainly order or class level. The community composition data do not always sum to 100% at all locations, owing to the presence of other taxa.

§ All samples were collected at the end of the growing season in 2008 (subarctic and boreal, late September; temperate and Mediterranean, October; and tropical, early December). Eight Kempson cores (21-cm diameter) and eight MacFayden cores (5-cm diameter) were taken at each field site. The reported data are based on extraction of the whole soil core (9-cm height), including the litter layer. Soil arthropods were extracted, counted and identified to the highest possible taxonomic level (families) (O.B. and S.S., unpublished observations).

Extended Data Table 7 | Analysis of variance testing for effects on total litter C loss (top) and N loss (bottom)

Source of variation	DF	SS	F	% Sum of Squares
	% C Loss			
Rapid decomposer (RD)	1	16580	290.7	3.9
Slow decomposer (SD)	1	12068	211.6	2.9
N-fixer (NF)	1	3146	55.2	0.7
Evergreen (EG)	1	3576	62.7	0.9
RD × NF	1	3532	61.9	0.8
RD × EG	1	747	13.1	0.2
SD × EG	1	1242	21.8	0.3
RD × SD	1	223	3.9	0.1
Decomposer community*	1	23404	410.3	5.6
Decomposer community × NF	1	907	15.9	0.2
Decomposer community × SD	1	526	9.2	0.1
Location†	4	50698	51.5	12.1
Location × EG	4	26247	115.0	6.2
Location × RD	4	13398	58.7	3.2
Location × SD	4	7784	34.1	1.9
Location × NF	4	8818	38.7	2.1
Location × RD × EG	4	1272	5.6	0.3
Location × RD × SD	4	1686	7.4	0.4
Location × SD × EG	4	976	4.3	0.2
Location × Decomposer community	4	31306	137.2	7.5
Location × Decomposer community × SD	4	1144	5.0	0.3
Ecosystem type (ET)†	1	27126	110.3	6.5
ET × Location†	4	26703	27.1	6.4
ET × Location × RD	5	1330	4.7	0.3
ET × Location × SD	5	1860	6.5	0.4
ET × NF	1	446	7.8	0.1
ET × Location × NF	4	554	2.4	0.1
ET × EG	1	3450	60.5	0.8
ET × Location × EG	4	2318	10.2	0.6
ET × RD × SD	1	262	4.6	0.1
ET × Decomposer community	1	7761	136.1	1.8
ET × Location × Decomposer community	4	8908	39.0	2.1
Block	40	9836	4.3	2.3
Residuals	2106	120133		28.6
	% N Loss			
Rapid decomposer (RD)	1	16570	87.7	1.4
Slow decomposer (SD)	1	31927	169.0	2.7
N-fixer (NF)	1	40390	213.7	3.5
Evergreen (EG)	1	3021	16.0	0.3
RD × NF	1	13245	70.1	1.1
RD × EG	1	2697	14.3	0.2
SD × NF	1	971	5.1	0.1
NF × EG	1	2438	12.9	0.2
RD × NF × EG	1	2947	15.6	0.3
Decomposer community*	1	48999	259.3	4.2
Decomposer community × NF	1	5281	28.0	0.5
Decomposer community × SD	1	1080	5.7	0.1
Decomposer community × EG	1	771	4.1	0.1
Decomposer community × NF × SD	1	1071	5.7	0.1
Decomposer community × NF × EG	1	2051	10.9	0.2
Location†	4	195881	66.7	16.8
Location × Decomposer community	4	75781	100.3	6.5
Location × NF	4	46245	61.2	4.0
Location × RD	4	30727	40.7	2.6
Location × EG	4	20789	27.5	1.8
Location × SD	4	4815	6.4	0.4
Location × NF × EG	4	10603	14.0	0.9
Location × RD × EG	4	3757	5.0	0.3
Location × NF × RD	4	3346	4.4	0.3
Location × Decomposer community × EG	4	2632	3.5	0.2
Ecosystem type (ET)†	1	16565	22.6	1.4
ET × Location†	4	92914	31.7	8.0
ET × RD	1	5845	30.9	0.5
ET × NF	1	1207	6.4	0.1
ET × Location × NF	4	9700	12.8	0.8
ET × EG	1	4173	22.1	0.4
ET × Location × EG	4	3870	5.1	0.3
ET × NF × RD	1	2554	13.5	0.2
ET × Location × RD × NF	4	1908	2.5	0.2
ET × NF × EG	1	1419	7.5	0.1
ET × Decomposer community	1	9015	47.7	0.8
ET × Location × Decomposer community	4	17968	23.8	1.5
Block	40	29349	3.9	2.5
Residuals	2106	397977		34.2

All terms included in the final model shown are significant at $P < 0.05$.

* The decomposer community was fitted as a log–linear contrast and not a factorial contrast (a factorial contrast is shown in Table 1).

† The location and ecosystem type and their interaction were tested against the block rather than against the residual.

Extended Data Table 8 | Analysis of variance testing for the proportional change in total litter N content

Source of variation	DF	SS	F	P
Mixture (decomposing alone or in presence of the other functional type)	1	0.002	0.057	0.81
Functional type (N-fixing or rapidly decomposing)	1	0.650	15.8	<0.001
Mixture × Functional type*	1	0.290	7.05	<0.01
Location†	4	2.053	11.9	<0.05
Ecosystem type (ET)†	1	0.818	18.9	<0.05
ET × Location†	4	2.277	13.1	<0.05
Block	4	0.173	1.05	0.38
Residuals	574	23.61		

The test compares specific two-species combinations, including the particular functional types of N-fixing and rapidly decomposing plants, to their respective single-species treatment across location and ecosystem type.
* A significant difference in the mixture × functional type interaction is taken as an indication of N transfer between litter species.
† Location and ecosystem type and their interaction were also included as factors in this analysis and were tested against the block rather than the residuals.

Extended Data Table 9 | Experimental duration and richness of naturally occurring local litter species in terrestrial and aquatic ecosystems at each of five widely dispersed locations

Ecosystem	Location	Incubation start	Incubation end	Duration (d)*	Natural litter species richness†
Terrestrial	Subarctic	22/ 09/ 06	5/ 09/ 08	714	6
	Boreal	20/ 10/ 06	12/ 05/ 08	570	4
	Temperate	17/ 01/ 07	5/ 03/ 08	414	1
	Mediterranean	15/ 11/ 07	19/ 10/ 08	338	4
	Tropical	20/ 11/ 06	25/ 08/ 07	278	7
Aquatic	Subarctic	27/ 07/ 07	11/ 10/ 07	76	6
	Boreal	11/ 09/ 07	13/ 11/ 07	63	4
	Temperate	18/ 10/ 07	13/ 12/ 07	56	4
	Mediterranean	16/ 11/ 07	3/ 01/ 08	48	11
	Tropical	9/ 05/ 07	14/ 08/ 07	97	10

* Incubation dates differed across ecosystem types and locations to ensure that, at the time of sampling, 40–50% of the mass of the most rapidly decomposing litter remained, thus allowing comparisons at similar decomposition stages.
† The mean species richness counts of naturally occurring litter in five randomly sampled plots that were the size of microcosms (15-cm diameter) in each of the five experimental blocks.