A general rule in ecology is that the abundance of species or individuals in communities sharing a common energy source decreases with increasing body size. However, external energy inputs in the form of resource subsidies can modify this size spectrum relationship. Here, we provide the first test of how a marine resource subsidy can affect size spectra of terrestrial communities, based on energy derived from Pacific salmon carcasses affecting a forest soil community beside streams in western Canada. Using both species-based and individual approaches, we found size structuring in this forest soil community, and transient community-wide doubling of standing biomass in response to energy pulses from Pacific salmon carcasses. One group of species were clear outliers in the middle of the size spectrum relationship: larval calliphorid and dryomyzid flies, which specialize on salmon carcasses, and which showed a tenfold increase in biomass in their size class when salmon were available. Thus, salmon subsidize their escape from the size spectrum. These results suggest that using a size-based perspective of resource subsidies can provide new insights into the structure and functioning of food webs.

1. Introduction

The availability and use of energy provide a fundamental limit to the abundance of species within communities [1–2]. These limits are determined not only by local abiotic and ecological factors such as primary production, temperature and species interactions, but also by an individual’s energy use, which is determined by its metabolic rate and body size [3–7]. This is largely because metabolic rate scales positively with body size ($M$) as $\sim M^{0.75}$ within a trophic level, constraining abundance ($N$) to scale negatively with body size as $\sim M^{-2.0}$ such that energy use is equivalent across size classes [8,9]. The resulting negative relationship between body size and abundance is arguably one of the best-known patterns in ecology.

Body size–abundance relationships are used in two main ways to understand community-wide patterns of energy use. The classical approach is to make comparisons among species. These show that smaller-bodied species can either be rare or abundant, while larger species can only be rare; hence species abundances tend to be constrained beneath an upper bound of energy limitation defined by the negative scaling of abundance with body size [10–12]. The second approach is to ignore species distinctions and make comparisons among all individuals pooled together. The resulting size distributions, called size spectra, are now commonly used in aquatic communities that are dominated by indeterminate growing organisms, and in terrestrial soil communities, where size may matter more than species identity [13–16]. As with the classical species-based approach, the size spectrum approach shows that summed individual abundances ($N$) scale negatively across log body size categories ($M$), as $\sim M^{-0.75}$ or steeper. This yields community $N \sim M$ scaling patterns that can parallel the

upper-bound slope defined by the species-level $N \sim M$ relationship [12]. These $N \sim M$ scaling relationships provide an important framework for understanding community structure and energy flow. However, little is known about how external subsidies of nutrients and energy may shape the $N \sim M$ relationship.

External resource subsidies may break the rules upon which body size–abundance relationships are founded, because multiple energy sources mean that even though individuals in communities may live together in space and time, their abundances will not be constrained solely by local productivity and the ecological interactions occurring within their community. For example, cross-system flows of nutrients and detritus can increase productivity across trophic levels, as shown by terrestrial carbon inputs to streams and lakes [17–19]. Furthermore, external energy subsidies may bypass the scaling rules if they enter food webs at higher trophic levels. For example, the migration of animals commonly subsidizes higher trophic levels such as the populations of local scavengers and predators [20,21]. Studies of resource subsidy effects generally show shifts in local species abundance that can alter community structure, but none have tested how subsidies may affect the size spectrum relationship. Taking a size-based approach, the intercept and/or slope of $N \sim M$ in communities can shift owing to changes in local resource availability, or through the coupling of benthic and pelagic food web compartments [22–24]. Large but transient outliers in abundance that depart from the linearity of the $N \sim M$ size spectrum have also been observed, which can cause trophic cascades and benefits for other species and size fractions [25,26].

Here, we provide a novel test for shifts in both the species-level and individual-level body size–abundance relationship of a forest soil community subsidized by the carcasses of Pacific salmon (Oncorhynchus spp.). Salmon return to spawn in thousands of streams throughout the Pacific Rim, which causes predator aggregations and can increase the productivity of nutrient-limited coastal watersheds [27,28]. Salmon-bearing ecosystems provide a unique opportunity to test the effects of resource subsidies on size spectra for two reasons: salmon spawning densities (here 20–30 tonnes ha$^{-1}$) are some of the highest biomass densities observed on Earth, and the availability of non-spawning areas plus the seasonality of salmon presence allows for good controls for understanding community-wide subsidy effects. Salmon subsidize adjacent forest soils through water transport of dissolved salmon nutrients (e.g. nitrogen + phosphorus), but also through active transport of salmon carcasses by bears (Ursus spp.) and other wildlife to riparian areas [29,30]. Salmon subsidies can thus affect forest soil communities in two ways: through nutrients entering the bottom of the food web and through specialists that are associated with the breakdown of salmon carcasses [31,32].

We contrast forest soil size spectra from before and during salmon spawning beside two streams that each support large runs of salmon versus control areas above waterfall barriers that prevent salmon migration. First, we hypothesized that temperate forest soil communities would be size structured, exhibiting a negative relationship between abundance and body mass. Second, we hypothesized that nutrients from salmon that enter the bottom of the food web would increase abundance across all size classes (increasing the intercept of the abundance–mass scaling relationship), and that these increases in abundance would remain year-round, including pre-spawning periods. Finally, we hypothesized that large-bodied carcass specialists would increase in abundance during salmon spawning, resulting in a transient shallowing of the $N \sim M$ slope when salmon are present. Overall, we show the utility of using size-based methods to evaluate the relative benefits of resource subsidies to species and individuals in food webs.

2. Material and methods

(a) Study sites

This study was conducted beside the Clatsop and Neekas rivers, near the Heiltsuk First Nation village of Bella Bella, on the central coast of British Columbia, Canada. Both streams remain minimally influenced by human disturbances, and are bisected by waterfalls 5–10 m high, resulting in a downstream area accessible to salmon and a similar salmon-free upstream reach, which for our purposes serves as a control. These waterfalls block salmon and limit the length of the salmon-bearing reach to 0.9 km on the Clatsop River and 2.1 km on Neekas River. Chum (Oncorhynchus keta), pink (Oncorhynchus gorbuscha) and coho (Oncorhynchus kisutch) salmon spawn from late August to early November, returning at average biomasses of 39 016 and 61 594 kg km$^{-1}$ to the Clatsop and Neekas spawning reaches, respectively, in the 10 years prior to sampling (1992–2001). Each year, an estimated 16–48 per cent of the chum salmon biomass and 4–6 per cent of the pink salmon biomass is transferred to the forest by black bears (Ursus americanus) and wolves (Canis lupus) [33].

(b) Forest soil community

We monitored a grid of pitfall traps to estimate the relative abundance of species in a forest soil community within 20 m of the Clatsop and Neekas rivers. Three $10 \times 10$ m plots were established both above (no salmon) and below (salmon) the waterfall barrier based on similarities in slope, canopy cover, forest structure and proximity to the waterfall in June prior to salmon spawning (pre-spawning) and in September during the spawning period (spawning) of 2001 [34]. Within each plot, we set up nine pitfall traps (each 10 cm diameter) in a $3 \times 3$ grid. Each trap was open for a total of 18 days (nine per season) and had three $15 \times 20$ cm drift fences to increase capture rates. Plots above versus below the waterfalls were separated by 300–600 m, limiting the likelihood of species dispersal among treatments.

All individuals caught in pitfall traps were sorted into the lowest taxonomic level possible in separate species categories (hereafter ‘species’) based on their feeding guild, life stage and body size [see the electronic supplementary material, table S1]. The greatest taxonomic diversity occurred within the Coleoptera, Diptera and Hymenoptera. Individual samples ($n = 1–188$) of each species were weighed to estimate species body mass ($M$). The abundance ($N$) of each species was summed across pitfall traps for each plot. The trap catch could be biased towards larger and more mobile individuals, which would result in a shallower than expected abundance–mass scaling. However, the replicated spatial and temporal contrasts provide a robust test of how a resource subsidy may affect a body size–abundance relationship sampled in a consistent (if slightly biased) manner using pitfall traps.

(c) Statistical description of species and individual $N \sim M$ relationships

We calculated both species and individual body size–abundance relationships of the forest soil community. First, the species-level
relationship was bounded using quantile regression to estimate the 90th quantile slope of $\log_{10}(\text{abundance})$ by $\log_{10}(\text{body size})$ of all species using the package ‘quantreg’ in R. Local size–density relationships are often characterized by constraint triangles or polygons where species inhabiting the outer boundaries are the most likely to reflect and define the limits of mass-specific energy availability [10–12]. The quantile regression technique provides a linear model at a given quantile, where the main decision to be made is which quantile(s) best represent the outer boundaries of the data [35]. We chose the 90th quantiles because although any particular quantile is correlated with those nearby, the 95th and 99th quantiles showed much greater sensitivity to outliers coupled with larger error terms.

Second, we calculated a size spectrum, more familiar to aquatic ecologists, by placing individuals, irrespective of species identity, within five $\log_{10}$ body size classes starting at the following sizes: $10^{-5}$, $10^0$, $10^1$, $10^2$ and $10^3$ mg, based on a range in body size of 0.1–3000 mg. The largest size class was truncated; however, our results are robust to changes in the number of size classes and the exclusion of the largest partial size class. Abundance was summed across all individuals in each class by plot and $M$ was given as the lower bound of each class. Because we used species mean masses, this assumes that there is only small variation in body size for each species relative to differences between classes, an assumption that would often be violated in more highly size-structured fish-dominated aquatic systems [13], but which is likely met here [16]. For example, one of the most variable species were cyclophorhaphan Diptera larvae, which ranged in mass from 8.0 to 54.2 mg ($n=188$, mean ± 20 mg), with 96 per cent of individuals falling within one $\log_{10}$ size class ($10^0$ mg = 10–100 mg), and only 4 per cent (seven of 188) falling in the previous $\log_{10}$ size class ($10^0$ mg = 1–10 mg).

We used generalized least squares to model the intercept and slope of $N \sim M$ of the individual size spectrum. This method is identical to linear regression, but allows us to account for spatial correlation in the model [36]. Because of the nested spatial design of the data, we applied a compound symmetry correlation structure of salmon (above waterfalls versus below waterfalls) within stream (Clatse, Neekas). This model thus behaves like a mixed-effects model, although it does not contain any random effects, and instead has a symmetrical dependence structure between communities surveyed on the same stream [36].

(d) Hypothesis testing and model selection

For both the species and the individual approaches, we used a model selection framework to test the effect of salmon subsidies on the $N \sim M$ relationship of the forest soil community. We used an initial full-fixed model that contained the main effects of season (June, pre-spawning; September, spawning), salmon (above waterfalls, no salmon; below waterfalls, salmon) and stream (Clatse, Neekas), and the a priori hypothesized interactions $M \times$ season, $N \sim M$ or $N \sim M$ and $M \times$ season $\times$ salmon. The interactions with $M$ tested for changes in the $N \sim M$ slope (e.g. changes in energy transfer between trophic levels), whereas the main effects and the season $\times$ salmon interaction tested for differences in the intercept (e.g. total energy available). We also tested the transience of the salmon subsidy effects; for example, system-wide increases in abundance across all size classes may occur only during the salmon spawning season (indicated by the season $\times$ salmon interaction). In comparison, salmon subsidies may disproportionately increase the abundance of large-bodied predators compared with smaller size classes, resulting in a shallower $N \sim M$ slope that remains throughout the year ($M \times$ salmon interaction), or only when salmon carcasses are available ($M \times$ season $\times$ salmon interaction).

We evaluated the relative strength of support of these hypotheses using an ‘all model combinations’ approach ($n = 38$ models), where model uncertainty was assessed using the Akaike information criteria (AICc) and multi-model averaging [37]. Models with lower AICc values have a better trade-off between complexity and fit than models with higher AICc scores. When there are several similarly weighted top models, model averaging can be used to incorporate the model uncertainty into the estimated parameters [37]. We used the MuMIn package in R, and the ‘zero’ method to compete models and calculate multi-model averaged parameter estimates from the set of models with $\Delta$AICc $< 4$ (see the electronic supplementary material, table S2) [38]. AICc weights ($w_i$) were calculated for each model (see the electronic supplementary material, table S3) and for each parameter to estimate relative variable importance (RVI). In the ‘zero’ method, a zero is substituted into the estimation of effect size when a given variable is absent from a model in the top model set, which thus decreases the multi-model parameter estimate (and error) of variables that only appear in models with low weights [38]. The number one ranked models and unstandardized parameter estimates are also shown in the electronic supplementary material, table S4. Because unstandardized parameter estimates (or coefficients) are only interpretable within the scale of each explanatory variable, we also compare relative effect sizes by centring each numeric variable (subtracting the mean) and dividing by two times the standard deviation [39]. This method allows reported coefficients (standardized parameter estimates) to be directly comparable with one another. All analyses were conducted in R v. 2.10.1 [40].

3. Results

Using a grid of pitfall traps, we caught and identified a total of 14 816 individuals from a forest soil community beside salmon spawning and control reaches, and during pre-spawning and spawning periods at two streams in coastal British Columbia. These were sorted into 104 species from at least 29 orders and 66 families, and were dominated by insects, arachnids, collembola and molluscs (see the electronic supplementary material, table S1). The dominant guilds included detritivores, predators and saprophages, followed by herbivores, fungivores and parasitoids.

Salmon arrival caused a transient doubling of the abundance and biomass of this forest soil community. During the autumn salmon spawning, pitfall traps in the salmon-bearing reaches below the waterfalls typically captured greater than twice the number of individuals and biomass compared with control reaches above waterfalls (figure 1). However, contrary to our original prediction, the abundance and biomass of these forest soil communities in the summer prior to salmon arrival was similarly lower between salmon-bearing and control reaches.

We found strong evidence for size structuring in this forest soil community using both species and individual approaches. At the species level, body size–abundance relationships showed a consistent triangular shape with wide-ranging abundance at small body sizes and low abundance of large-bodied species (figure 2a,b; electronic supplementary material, figure S1). There was a consistent outer-bound slope across the 90th quantile of abundance, which scaled negatively with body size as $N \sim M^{-0.30}$ (see the electronic supplementary material, table S2). At the individual level, abundance scaled negatively with body size as $N \sim M^{-0.59}$ when the abundance of all individuals were summed across five $\log_{10}$ body size classes (figure 2c,d; electronic supplementary material, figure S2 and table S2).
without salmon, although this only occurred during the salmon spawning season (strong season × salmon interaction; table 2). The individual effects of salmon and season were found in all models with AICc < 4 (RVI = 1), and the interaction between season and salmon was also important (species model: RVI = 1; individual model: RVI = 0.91). By contrast, we observed little support for changes in the relative abundance among size classes as would be diagnosed by shifts in the body size–abundance slope with subsidies of salmon (low RVI and standardized estimates for M × season, M × salmon and M × season × salmon; table 2). While there were differences in intercept between streams (species model: RVI = 0.66; individual model: RVI = 1), our findings were consistent across streams (see the electronic supplementary material, figures S1 and S2). The top models of the species (w = 0.25) and individual analyses (w = 0.54) both contained the same parameters (see the electronic supplementary material, tables S3 and S4).

4. Discussion

We have shown that energy flow across species and individuals is size structured in forest soil communities beside streams in a temperate rainforest in western Canada. We also show that a resource subsidy, with energy derived from Pacific salmon carcasses, causes a transient doubling of the standing biomass of these communities when salmon are available, and enables salmon carcass-specialist species—fly larvae that have fed on salmon carcasses—to reach higher than expected abundances, and hence escape the local size spectrum. Counter to our original hypotheses, salmon subsidies did not disproportionately benefit larger size classes, nor affect the biomass of the food web throughout the year, but affected a guild of carcass specialists that are intermediate in size, and hence reside in the middle of this size spectrum.

Size structuring was found using both species- and individual-based approaches. While fish-dominated aquatic systems are well known to be size structured [13,14], examples in terrestrial communities are less common. Several studies have demonstrated size structuring across trophic levels in soil communities, where species and/or individuals use similar amounts of available energy [15,16,41]. Using a species-based approach, we found a consistent triangular shape to a local forest soil community, with many rarer species and several dominant ones bounded by an outer slope of M~−0.50. This triangular shape can occur because local species abundance distributions are often right-skewed, with only a few very abundant species and many rarer ones [42,43]. For example, species tend to be abundant in a small portion of their range and rarer elsewhere [44]. The community dominants are thus most likely to be experiencing energy limitation [10–12], whereas rarer species may have more specialized niches with different energy sources, or may have other ecological limits such as competition [45] or predation [46].

An alternative to the species approach is to sum abundance across individuals of different sizes. Using an individual approach, we found a scaling of M~−0.59, and similar top models to the 90th quantile approach with all species. Across trophic levels in individual size spectra, it is predicted that inefficient energy transfer will yield steeper
Figure 2. (a,b) Species and (c,d) individual body size (M) – abundance (N) relationships in forest soil communities (a,c) beside streams with spawning Pacific salmon and (b,d) above waterfall barriers without salmon. When salmon carcasses are available, we observe systemic increases in the intercept, and specialist species—fly larvae that have consumed salmon carcasses—escaping the size spectrum of this forest soil community. N ~ M relationships were modelled across the 90th quantile of abundance for all species in the community, and by summing across all individuals within five \( \log_{10} \) body size categories. Surveys occurred in two time periods: in early summer before salmon have arrived (open circles and dotted lines), and in the autumn when salmon spawn (solid lines and filled circles).

Abundance is averaged across two streams, and lines are fitted from multi-model parameter estimates (see the electronic supplementary material, table S2). Pictures relate to the nearest data points and highlight several of the major species/groups sampled along the gradient in body mass (collembola: *Ptenothrix maculosa*; flies: cyclorrhaphan Diptera larvae; spiders: *Cybaeus reticulatus*; slugs: Arionidae spp.).

Table 1. Average proportional change in abundance and biomass by individual \( \log_{10} \) body size class (mg) in forest soil communities subsidized by salmon compared with control reaches with no salmon. Sampling occurred in autumn salmon spawning and in early summer during pre-spawning. Abundance (N) and biomass (B) ratios = N or B below waterfalls with salmon/N or B above waterfalls with no salmon.

<table>
<thead>
<tr>
<th>season</th>
<th>( \log_{10} ) body size class (mg)</th>
<th>abundance ratio</th>
<th>biomass ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>autumn (during spawning): (spawning reach/control reach)</td>
<td>0.1 – 1</td>
<td>1.36</td>
<td>1.55</td>
</tr>
<tr>
<td></td>
<td>1 – 10</td>
<td>1.14</td>
<td>1.37</td>
</tr>
<tr>
<td></td>
<td>10 – 100</td>
<td>19.95</td>
<td>10.71</td>
</tr>
<tr>
<td></td>
<td>100 – 1000</td>
<td>2.23</td>
<td>2.11</td>
</tr>
<tr>
<td></td>
<td>1000 – 10 000</td>
<td>0.60</td>
<td>0.56</td>
</tr>
<tr>
<td>summer (pre-spawning): (spawning reach/control reach)</td>
<td>0.1 – 1</td>
<td>0.99</td>
<td>1.18</td>
</tr>
<tr>
<td></td>
<td>1 – 10</td>
<td>0.62</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>10 – 100</td>
<td>0.84</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>100 – 1000</td>
<td>2.26</td>
<td>1.51</td>
</tr>
<tr>
<td></td>
<td>1000 – 10 000</td>
<td>0.33</td>
<td>0.31</td>
</tr>
<tr>
<td>autumn ratio/summer ratio</td>
<td>0.1 – 1</td>
<td>1.38</td>
<td>1.32</td>
</tr>
<tr>
<td></td>
<td>1 – 10</td>
<td>1.84</td>
<td>2.13</td>
</tr>
<tr>
<td></td>
<td>10 – 100</td>
<td>23.78</td>
<td>14.34</td>
</tr>
<tr>
<td></td>
<td>100 – 1000</td>
<td>0.98</td>
<td>1.39</td>
</tr>
<tr>
<td></td>
<td>1000 – 10 000</td>
<td>1.80</td>
<td>1.79</td>
</tr>
</tbody>
</table>
were transient and only observed when salmon were
our predictions, the increases in the size spectrum intercept
in abundance across all size classes. However, contrary to
hypothesis that salmon subsidies cause systemic increases
such as earthworms [16]. We found evidence for our initial
study that organic farms can increase the abundance of detritivores
when salmon are not present [50]. For example, long-term subsidies
to detritivores and predators, including in summer when
these nutrient effects may influence the abundance of soil
through links between above- and below-ground biota,
gen content and growth of associated forests [48,49].

Table 2. Relative variable importance (RVI) and standardized parameter estimates (std.est.) predicting species and individual abundance in forest soil communities subsidized by Pacific salmon carcasses. Greater relative variable importance was observed for shifts in the intercept than for shifts in the slope with salmon subsidies.

<table>
<thead>
<tr>
<th>method</th>
<th>parameter</th>
<th>test of</th>
<th>RVI</th>
<th>std.est.</th>
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<tr>
<td>species size–density relationship 90th quantile regression</td>
<td>body mass (M)</td>
<td>slope</td>
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<td>salmon</td>
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<td>0.11</td>
<td></td>
</tr>
<tr>
<td>season</td>
<td>intercept</td>
<td>1</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>stream</td>
<td>intercept</td>
<td>0.66</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>salmon × season</td>
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<td>−0.28</td>
<td></td>
</tr>
<tr>
<td>M × season</td>
<td>slope</td>
<td>0.13</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>M × salmon</td>
<td>slope</td>
<td>0.52</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>M × salmon × season</td>
<td>slope</td>
<td>0.32</td>
<td>−0.11</td>
<td></td>
</tr>
<tr>
<td>individual size distribution generalized least squares</td>
<td>body mass (M)</td>
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<td>−1.67</td>
</tr>
<tr>
<td>salmon</td>
<td>intercept</td>
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<td>0.23</td>
<td></td>
</tr>
<tr>
<td>season</td>
<td>intercept</td>
<td>1</td>
<td>−0.10</td>
<td></td>
</tr>
<tr>
<td>stream</td>
<td>intercept</td>
<td>1</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>salmon × season</td>
<td>intercept</td>
<td>0.91</td>
<td>−0.24</td>
<td></td>
</tr>
<tr>
<td>M × season</td>
<td>slope</td>
<td>0.19</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>M × salmon</td>
<td>slope</td>
<td>0.19</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>M × salmon × season</td>
<td>slope</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

scalings of \( N \sim M \) (e.g. \( M^{-1.2} \)), an observation common in
aquatic food webs [13]. However, declines in species diversity
with increasing body size can also compensate for inefficient
energy transfer between trophic levels, bringing scalings
closer to \( M^{-0.75} \) [16]. In forest soil communities, shallow
slopes across the individual size distribution (mean = \( M^{-0.44} \))
are common, which may be because of higher than expected
trophic transfer efficiency [16]. Alternatively, it could be
because of fractional predator–prey mass ratios, as found in
other detrital systems such as marine benthic infauna, where
larger individuals feed at lower trophic levels and have greater
relative access to available energy [47]. Thus, the expected
slope of forest soil communities remains an open question,
although we remain cautious about the interpretation of our
slope of \( M^{-0.39} \), because pitfall traps may tend towards
increased catch of larger individuals.

Here, we show how size spectra can be used to detect
and contextualize the beneficiaries of resource subsidies.
We hypothesized that salmon subsidies would increase the
standing biomass across the community (the intercept)
year-round, and cause transient increases in abundance of
larger-bodied scavengers and predators (shallowing of the
slope) when salmon are available. In riparian areas beside
salmon streams, the nutrients provided by spawning
salmon can shift plant communities, and increase the nitrogen
content and growth of associated forests [48,49].
Through links between above- and below-ground biota,
these nutrient effects may influence the abundance of soil
detritivores and predators, including in summer when
salmon are not present [50]. For example, long-term subsidies
to organic farms can increase the abundance of detritivores
such as earthworms [16]. We found evidence for our initial
hypothesis that salmon subsidies cause systemic increases
in abundance across all size classes. However, contrary to
our predictions, the increases in the size spectrum intercept
were transient and only observed when salmon were
available. Further, salmon subsidies did not affect the
distribution of that abundance (the slope). This means that
shifts in the soil food web occur primarily in the short
term, with energy ultimately derived from salmon, where
species across a range of body sizes benefit. When salmon
are not available, the community below the waterfall barrier
then relaxes to the same scaling relationship as above the
waterfalls, where salmon are always absent [51].

Strong competition for subsidized resources often favours
species with specialized life history and mobility traits that
enable a quick response to subsidies [52]. These transient out-
liers in numbers at mass occur commonly in aquatic systems,
for example through upwelling events, which can then cause
cascading mesopredator release effects for other species
[25,26]. We observed transient 20-fold increases in abundance
and 10-fold increases in biomass within an intermediate size
class when salmon were available compared with control
sites with no salmon. Ninety per cent of these increases are
composed of one species group (cyclophragmin fly larvae),
which escape the size spectrum of this forest soil community.
Fly larvae are commonly observed as dominant consumers of
salmon carcasses and are a key part of the streamside food
web [29,31,33,53]. They overwinter in the soil near carcasses
for at least eight months, and during this time are consumed
by at least 21 soil invertebrate and 16 vertebrate species [33],
including large-bodied species such as the carrion beetle
Nicrophorus investigator, but also small-bodied parasitic
wasps and rove beetles (Family Staphylinidae). In the late
spring and summer, the surviving larvae pulate into adult
flies and emerge from the soil en masse, which can affect
the bloom timing of local plant species [54], and provides
one mechanism by which top predators such as songbirds
may have higher densities along these same salmon streams
and estuaries [55–57].

In summary, we illustrate how body size–abundance dis-
tributions can be used as a framework for evaluating the food
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