Manuscript Template

H1 FRONT MATTER

H2: Title

- Full title: Terrestrial support of lake food webs: synthesis reveals controls over cross-ecosystem resource use
- Short title: Terrestrial support of lake zooplankton

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H2:Abstract

Widespread evidence that organic matter exported from terrestrial into aquatic ecosystems supports recipient food webs remains controversial. A pressing question is not only whether high terrestrial support is possible but what the general conditions are under which it arises. Here we assemble the largest dataset to date of the isotopic composition (δ^2H, δ^{13}C, δ^{15}N) of lake zooplankton and the resources at the base of their associated food webs. In total, our dataset spans 559 observations across 147 lakes from the boreal to subtropics. By predicting terrestrial resource support from within-lake and catchment-level characteristics, we found that half of all consumer observations (i.e. median) were comprised of at least 42% terrestrial-derived material. Terrestrial support of zooplankton generally was greatest in lakes with large physical and hydrological connections to catchments that were rich in above- and below-ground organic matter. However, some consumers responded less strongly to terrestrial resources where within-lake production was elevated. Our study shows that multiple mechanisms drive widespread cross-ecosystem support of aquatic consumers across northern hemisphere lakes and suggests that changes in terrestrial landscapes will influence ecosystem processes well beyond their boundaries.

H1 MAIN TEXT

H2:Introduction

Ecosystems are linked across landscapes by the flow of energy and nutrients (*1*). This has long been evident at the scale of catchments, wherein terrestrial organic matter (t-OM) is collected by hydrological flow and funnelled into receiving waterways at lower elevation. Aquatic organisms are consequently able to use material produced outside the boundaries of their habitat – a process known as allochthony – to support their metabolic demands (*2*). Accumulating evidence now suggests that the use of terrestrial-derived resources can be as high as 40 to 94% in some aquatic food webs (*3–13*). Cross-ecosystem resources therefore play an important role in supporting ecosystem functioning and the delivery of key ecosystem services, such as fish production (*9*, *14*). Yet it remains unclear as to how reliance upon these resources will change with continued human degradation or alternatively restoration of the planet's landscapes.

Generalising how cross-ecosystem resources support lentic consumers in particular has been controversial (*6*, *15–16*). In addition to grazing on phytoplankton and microbial organisms that decompose detritus generated within aquatic ecosystems, zooplankton ingest microbes that metabolize t-OM and they directly uptake t-OM through feeding (*17–19*). These t-OM sources can sustain consumer growth and reproduction as long as some high-quality resources, such as green algae, are present (*15*, *19*). However, t-OM is generally a poor quality resource. It lacks essential fatty acids and macronutrients available from algae (*15*, *20*). Rather, t-OM likely supplements existing within-lake resources as it becomes increasingly available (*9*) and/or the latter are limited, e.g. seasonally (*3*, *21*), elevating allochthony without necessarily increasing consumer production (*16*, *22–24*).

Low levels of allochthony (<20%) in some studies of lake food webs have also cast doubt on the importance of cross-ecosystem resources in supporting consumer biomass (*25–27*). This leaves considerable variation to be explained among studies, both within and across geographic regions (*8*, *21*, *28–29*). Nonetheless, theory and meta-analyses of consumer abundances can be used to predict that

allochthonous resource fluxes will be most utilised when (i) receiving food webs have low productivity or relatively few resources, (ii) the delivery potential of donor habitats is relatively large, and/or (iii) consumers have weak preferences for autochthonous resources (*30–32*). The relative importance of spatial energy flows will also depend on temporal variation in food web structure, such as arising from seasonal changes in primary production (*33*). Therefore, previous disagreements over the importance of terrestrial support may have simply arisen because lakes differ in their productivity either spatially and/or temporally, are surrounded by different land uses, and have different zooplankton assemblages. Empirically testing these general predictions across diverse habitats can help reconcile contrasting findings.

Finally, controversy has arisen over the methods used to measure allochthony, which are primarily based on stable isotope mixing models (*15*, *34–35*). Rigorous simulation approaches are now needed to understand how mixing models perform under different empirical conditions and identify potential sources of bias, such as in end member determination. Taken with concerns around the nutritional quality of t-OM and large variability in observed allochthony, the general conditions under which terrestrial resources are important to lake food webs remains to be identified. Accordingly, such an analysis can also reveal the conditions wherein the use of autochthonous resources varies.

Here we test how within-lake processes and catchment-level characteristics jointly influence the use of terrestrial and within-lake resources in aquatic food webs, thereby explaining the large variation in allochthony reported to date. As our study sites were a non-random collection of monitoring lakes for which terrestrial resources were likely more important, on average, than elsewhere, we focused on understanding when, and for which consumers, allochthony was high in our subset of global lake types. We do so by simultaneously testing five mutually-inclusive hypotheses around cross-ecosystem resources and comparing their relative support:

Favourable resources hypothesis: Allochthony decreases when more high-quality resources, i.e. algae, are produced (*5*, *21*).

Catchment deposition hypothesis: Allochthony increases as more t-OM is exported from the surrounding catchment. A greater quantity and reactivity of t-OM can be made available for consumption by consumers at the base of aquatic food webs as the coverage and density of labile vegetation and soil carbon in the surrounding catchment increase (*9, 36*). A larger land-water interface can also increase the geomorphic potential of catchments to deliver t-OM into receiving food webs (*14, 37*).

Algal subtraction hypothesis: Allochthony increases with the availability of t-OM where algal production becomes limited by shading more than it benefits from the nutrients associated with t-OM (*38*).

Consumer preference hypothesis: Allochthony increases in consumers such as *Cladocera* that are relatively effective grazers of bacterial decomposers and t-OM as these resources become increasingly available (*28, 39–40*).

Seasonality hypothesis: Allochthony increases outside of the summer growing season when plant litter production peaks and/or within-lake production is negligible (*3, 40–41*).

Our analysis is the first global effort explicitly linking resource use by aquatic organisms to catchment characteristics such as land cover. We collated stable isotope (δ^2H, δ^{13}C, δ^{15}N) measurements taken year-round for 559 observations of pelagic consumers across 147 lakes in many of the planet's freshwater hotspots. Using a uniform approach to delineating study catchments, we also assembled an extensive database on surrounding land use, geomorphology, and water chemistry derived from satellite and field data. We then estimated terrestrial resource use (φ_T) in an isotopic mixing model by relating φ_T to within-lake and catchment characteristics using structural equation modelling (SEM) (Supplementary Methods S1, S2). SEM allows us to test explicitly the strength and direction of five of the major hypotheses about allochthony. Previously, we have shown that bias in the mixing model approach is minimal (*7, 9, 42*), and we expand upon these analyses to show that it is relatively insensitive both to the range of isotopic values observed in our dataset and missing data sources.

H2: Results

Isotopic mixing model performance

The isotopic mixing model that we developed had sufficient power to test our focal hypotheses because it strongly recovered known values of φ_T and its response to extrinsic factors. We simulated datasets that replicated our empirical observations with known effect sizes and found that posterior distributions for the effects of lake- and catchment-level characteristics on φ_T averaged across 100 simulations were tightly centred on their 'true' values (dotted lines vs polygons in Figs. 1a,b). φ_T was also recovered with relatively high precision and accuracy (Fig. 1c). While there was a tendency to overestimate moderate values of φ_T (ca. 0.20–0.35) with a relative bias, on average, of up to 22% (absolute deviation in φ_T of 8%), most relative bias was small and ranged between -10 to 10% (Fig. 1d). Data for $\delta^2 H$ isotopes reduced this bias further (Fig. 1d), because it most strongly differentiated between our two basal food sources of terrestrial plants and pelagic phytoplankton (fig. S1 in Supplementary Methods S2).

We also considered whether our results could be biased by the different basal food resources and isotopes that we studied. Isotopic signatures of terrestrial resources loaded into food webs, measured from fresh or senesced leaves of the dominant plants or soil OM in surrounding catchments, varied little as compared with within-lake resources (fig. S1 in Supplementary Methods S2). Pelagic phytoplankton, which were directly measured for n = 333 consumer observations and estimated in another n = 226 from their discrimination between $\delta^2 H$ and $\delta^1 H$ in dietary water, varied much more in $\delta^{13} C$ and $\delta^{15} N$, though with no clear difference between the two methods of characterising isotopic signatures (fig. S1 in Supplementary Methods S2). Nonetheless, the variation in the observed resources had little influence on our results. We found that bias in both φ_T and its response to lake- and catchment-level characteristics was unchanged when we increased the uncertainty in the allochthonous and autochthonous resources that were input into the mixing model (light and dark green lines no different from grey box in fig. S2 in Supplementary Methods S3). Additional simulations showed that all focal parameters were relatively

insensitive to increased uncertainty in other sources, such as the isotope measurements themselves (fig. S1 in Supplementary Methods S3), biased prior information about consumer physiology (fig. S2 in Supplementary Methods S3), and potentially missing resources that would bias determination of the within-lake resources, such as methane oxidising bacteria (fig. S3 in Supplementary Methods S3).

Mechanisms underlying resource use

Given our validated model, we found that φ_T estimated for aquatic consumers based on empirical δ^2H, $\delta^{13}C$, and $\delta^{15}N$ data varied greatly across gradients of water quality and catchment characteristics (Fig 2; see Supplementary Data S1 for site summaries). Mean (95% CI) estimates of consumer biomass derived from terrestrial resources ranged between 11% (3-21%) to 83% (72-92%) across 147 lakes, with a median of 42% (Fig. 2). The model generating these estimates fitted the empirical data very well (Bayesian R^2 ranging from 0.64-0.99 across observations in the one-, two-, and three-isotope models; fig. S2 in Supplementary Methods S2). As the estimates were sampled using Bayesian inference, we also generated a posterior distribution of φ_T for each of our 559 consumer observations. The resulting distributions were always peaked with almost all coefficients of variation <0.4 (fig. S3 in Supplementary Methods S2), emphasising low uncertainty in our predictions.

For the first time, we could link the large variation in φ_T found in Fig. 2a and across previous studies to explicit mechanisms that predicted when autochthonous versus allochthonous resources would be important. We did so by connecting the distributions of φ_T for each consumer observation to within-lake and catchment characteristics and estimating whether the associated 95% credible intervals (CIs) excluded zero, shown as green and blue arrows for positive and negative effects, respectively, in Fig. 3. First, we found that support for the catchment deposition hypothesis operated via both particulate organic carbon (POC) exported from woody vegetation, while accounting for variation in terrestrial litter decomposition because of warmer temperatures, and dissolved organic carbon (DOC) contributed by catchments with dense vegetation cover, rich soil carbon pools, and a high degree of soil wetness (green

lines for all connections in Figs. 3, 4a,b). Greater quantities of t-OM subsequently elevated allochthonous resources (i.e. summed contribution of terrestrial-derived DOC and POC), thereby increasing allochthony (Fig. 3). For example, a 30% increase in allochthonous resources over their observed range increased φ_T in summer by a relative mean of 7% across all taxa (95% CI: 1-14%) when other effects were at their mean levels (Fig. 4c). We also found that φ_T increased as lakes were smaller relative to their shoreline, as predicted by the catchment deposition hypothesis (green arrows connecting LP:LA to φ_T in Fig. 3). Support for the catchment deposition hypothesis persisted with other indicators of terrestrial influence, especially when we considered lake perimeter in the analyses (Supplementary Methods S3). Second, we found that the positive response of φ_T to increasing allochthonous resources was reduced by increasing within-lake productivity (i.e. interaction with chlorophyll *a*) for *Daphnia* and bulk zooplankton (Fig. 5), as predicted by the favourable resources hypothesis (Fig. 3), but this was not supported across all taxa. Third, the interactive effect was weakened as more allochthonous resources shaded the water column and reduced algal productivity consistent with the subtraction hypothesis (blue line connecting colour to chlorophyll in Fig. 3).

Finally, there were clear differences across consumers and seasons in the use of allochthonous resources, as predicted by the consumer preference and seasonality hypotheses, respectively. Less-selective filter feeders such as *Daphnia*, which also often comprised much of the biomass in the Cladocera and bulk zooplankton categories, had greater φ_T as allochthonous resources were increasingly available (95% CIs excluding zero, Fig. 5a), but less so where chlorophyll *a* concentrations were high (Fig. 5b). φ_T in *Chaoborus*, which integrate the signals of multiple prey items, also responded positively to the availability of allochthonous resources (Fig. 5a). By contrast, more selective suspension feeders such as the calanoids, including *Eudiaptomus*, did not have a greater φ_T as allochthonous resources became more available (95% CIs overlapping zero, Figs. 5a,b). There was no difference in φ_T across consumers at the mean water chemistry conditions (Fig 5c). We also found that mean levels of allochthony were greatest during autumn, when plant litter production peaks, and winter, when within-

lake production is minimised (95% CI for difference from summer: 0.36-0.77 and 0.20-3.1, respectively; Fig. 3).

An important benefit of our modelling approach is that it allowed us to compare relative support for different hypotheses. For each hypothesis except that of consumer preference, we calculated the change in φ_T with an increase in a focal variable from one SD beneath to one SD above its mean, whilst all other variables were fixed at mean levels. This revealed that DOC and the ratio of lake perimeter to lake area (an indicator of t-OM delivery potential) had the strongest cumulative effects in our network of interacting mechanisms (Fig. 3), increasing φ_T by between 1 to 13% through their effects on the availability of allochthonous resources.

H2: Discussion

Our analysis across lakes from the boreal to subtropics shows that terrestrial resource use is unequivocally important, accounting for at least 42% of consumer biomass in half of all observations, though high levels of allochthony (e.g. >60%) are not a general pattern. Concurrently, we have discovered the conditions that make high allochthony possible, helping to explain the tremendous discrepancy observed across stable isotope studies of lake food webs over the last two decades (*6–8*, *16*, *21*, *23*, *25–26*, *28*). While the lowest mean estimate of allochthony reported here of 11% exceeds that observed by others, this may be because our non-random sample of study sites largely lacked clear deep-water and eutrophic lakes where primary production is relatively high (*5*, *25*). Our results also offer general insights for understanding the fate of spatial resource fluxes because we have found that allochthonous resources are more utilised, as determined using stable isotope tracers, in ecosystems that are unproductive and/or well connected to donor habitats. Predictable changes in allochthony along continuous gradients, such as in hydrological connectivity and ecosystem productivity, support theoretical predictions for when cross-ecosystem resources will be most utilised (*30–32*), but have only been empirically reported to our knowledge in two much more local studies (*9*, *14*).

Mechanisms Underlying Allochthony

We found support for the favourable resources and catchment deposition hypotheses. These hypotheses suggest that levels of allochthony in freshwater lakes depend on the quantity of terrestrial organic matter (t-OM) that is delivered into food webs relative to the amount of internal production. It is therefore unsurprising that striking differences in allochthony have previously been reported across lakes that span gradients of trophic state, morphometry, and catchment characteristics (*8*, *21*, *25*; *28–29*). Relative exposure of lakes to their surrounding shorelines was an especially important characteristic for driving support for the catchment deposition hypothesis and highlighted the importance of nearshore processes for t-OM export (*43*). Our results also show that allochthony is promoted by dissolved and particulate t-OM. This finding suggests that direct ingestion of particulate organic matter and its associated biofilms as well as bacterial decomposition are both key for transferring t-OM into aquatic food webs.

Algal production attenuated the effects of increasing allochthonous resources on terrestrial resource support for some consumers, as expected if it is a higher quality and more preferred resource (*15*, *20*), but this effect was sensitive to shading of the water column (i.e. algal subtraction hypothesis). These responses are likely to reflect shifts in the availability of phytoplankton across depth zones as water clarity changes. In deep clear lakes, few of which we studied here, phytoplankton may support the majority of zooplankton biomass (*25*). As t-OM increases, reduced light penetration and shallower thermoclines will constrain metalimnetic phytoplankton, decreasing its support of zooplankton (*44*). By contrast, concentrations of DOC comparable to those observed in our dataset may be sufficient to promote primary productivity in the epilimnion by contributing limiting nutrients without reducing the average amount of radiation reaching phytoplankton cells (*45*). The effects of algal production on allochthony will also vary seasonally (*3*, *40–41*), as observed here (i.e. seasonality hypothesis). Allochthony was specifically lower during spring and summer when algal production was maximised than during autumn leaf-fall or winter.

Responses to terrestrial and within-lakes resources by the most abundant taxa in our dataset were generally consistent with known feeding strategies. For example, calanoids preferentially consume phytoplankton and thus do not respond strongly to direct increases in terrestrial resources (*28*, *40*), as we found here. Terrestrial resource use may also change little with small increases in within-lake production if it is already minor (<20%) at low phytoplankton biomass. By contrast, *Daphnia* and cyclopoids benefited from more terrestrial resources because they can graze heterotrophic bacteria associated with dissolved t-OM (*46–47*), even during periods of high primary production (*40*). However, only *Daphnia* reduced their intake of allochthonous resources with increasing chlorophyll *a*. *Daphnia* are more likely to ingest larger particulate material from leaf fragments or flocculated DOC than calanoids (*28*). As these materials are poorly assimilated during growth (*15*, *20*), they should be less utilised when phytoplankton are available. The lack of an association with chlorophyll *a* in other taxa may be unsurprising if terrestrial resources only sustain growth when supplemented with algae (*15*, *19*). An increasing supply and uptake of algae could thus result in a greater uptake of terrestrial resources without necessarily changing the proportional use of these two resources. Finally, allochthony of the invertebrate predator *Chaoborus* appeared more responsive to terrestrial resources than some of the zooplankton grazers that it preys upon, e.g. *Bosmina*. This may have arisen because we selected early instars that ingest proportionally more rotifers, which are enriched in allochthonous resources (*28*), than larger zooplankton, such as *Daphnia* (*47*). *Chaoborus* can also assimilate fewer grazers and more detritivores where they reside in the hypolimnion, such as in lakes with planktivorous fish (*5*). More generally, spatial variation in cross-ecosystem resources should lead to different patterns of allochthony between migratory and more stationary consumers (*1*).

While we have found support for general mechanisms underlying allochthony, our study sites only partially captured the range of lake physical and chemical characteristics observed globally and within our focal study regions (e.g. *48–49*). Three notable differences emerge from comparisons with global datasets. First, >90% of the world's lakes have been estimated to be <0.01 km^2 versus 34% in

our dataset (*50*). Most of our lakes were slightly larger with areas between 0.01-1 km^2 (fig. S6 in

Supplementary Methods S1). Second, median DOC concentrations in our dataset were slightly higher

than in a compilation of 7,514 lakes spanning large biogeographic gradients (*51*): 6.9 vs 5.7 mg L^{-1},

respectively, suggesting that we may be slightly overestimating the extent of allochthonous inputs and

their shading effects (fig. S7 in Supplementary Methods S1). Finally, median chlorophyll *a*

concentrations in our dataset were nearly 40% lower than satellite-derived estimates in 80,012 lakes

(*52*): 4.7 vs 7.5 mg L^{-1}, respectively, over-representing oligotrophic lakes where allochthony might be

higher (fig. S8 in Supplementary Methods S1). The strength of support for some of the mechanisms that

we detected might therefore vary in lakes with markedly different characteristics though remain

generalizable in many other cases.

Improving Predictions of Cross-Ecosystem Resource Use

We found that estimates of terrestrial resource use were positively biased by an average of up to 22% on

a relative basis (ca. 8% on an absolute scale). Extending our analysis across the entire range of potential

φ_T, rather than only the range observed in the empirical dataset, revealed that this problem was

exacerbated as φ_T approached 0 (fig. S4 in Supplementary Methods S3). This was because sampling φ_T

from a Beta distribution meant that values could not be <0, thereby limiting negative bias from accruing.

Similarly, bias was mostly negative as φ_T approached 1 (fig. S4 in Supplementary Methods S3), again

because φ_T could not be >1. Statistical methods for inferring isotopic compositions can do little to

account for this given inherent constraints in φ_T. Caution is therefore needed in emphasising the

importance of allochthony at extremely low and high values. Estimating cross-ecosystem resource use

by enriching distinctions in the isotopic composition of resources (e.g. *4*, *53*) and measuring additional

source-specific biomarkers, such as fatty acids (*27*), may be particularly helpful in these circumstances

by reducing underlying isotopic variation and better constraining models to data.

We have also expanded our understanding of the performance and bias of isotopic mixing models (*7*, *9*, *42*), which have been previously critiqued without rigorous statistical tests (*15*, *34–35*). For end members, we found little difference between isotopic signatures of pelagic phytoplankton that were directly measured versus inferred from the known discrimination of producers for ^{2}H relative to ^{1}H in surrounding water, supporting the use of this approach to assign isotope values (*54*). We similarly found little variation in terrestrial resources despite sometimes measuring either live, recently senesced, or decomposed leaf material. The δ^2H, δ^{13}C, and δ^{15}N values of fresh leaves have been shown to change little as they decay, supporting our grouping of terrestrial material in different states of decomposition (*54*). Bias in the recovery of model parameters was also relatively insensitive to increased uncertainty in the end member isotope values and physiological parameters used to infer dietary water uptake, as well as moderate levels of missing within-lake resources. Our widespread measurement of δ^2H for 79% of consumer observations likely helped to reduce bias by clearly differentiating between the isotopic signature of aquatic and terrestrial primary production (*55*). Overall, our analyses highlight the robustness of mixing models and offer opportunities to parameterise them with new types of data, such as fatty acid profiles (*27*).

New Connections in Managing Land And Water Resources

Our findings emphasise that better integration is needed across ecosystems in management. We found that consumers rely heavily on terrestrial resources in lakes that are surrounded by relatively long shorelines with dense vegetation and soil carbon stores. This provides empirical support for the conventional wisdom, largely from riparian systems (*56*, *57*), that even small land cover change along lakeshores impacts aquatic food webs. Where consumer production benefits from terrestrial resources, our results suggest that reductions in forest cover and soil carbon can reduce the delivery of important services provided by planktonic communities, such as fish production (*9*) or control of algal growth (*58*). Of course, consumers with high terrestrial resource use will not necessarily be more productive.

This depends on whether t-OM displaces higher quality within-lake resources by shading (*16*, *22–23*, *38*) or simply adds more of a suitable food source to the environment (*9*, *19*).

More broadly, our work reveals how terrestrial landscapes influence ecosystem functioning well beyond their boundaries. Much of the north temperate land mass, which stores most of the world's freshwater, is changing with shifts in climate, natural disturbances, and human activities (*59*). For example, increases in historical fire frequency across the boreal is clearing forest twice as quickly as it is being gained (*60*). Such changes will clearly impact receiving waters. Our analysis therefore strengthens the need for catchment-level approaches to the management of land and water resources in a changing world.

H2: Materials and Methods

Sample Collection

We sampled 147 lakes on 1 to 5 occasions during at least the summer growing season or autumn, and, where possible, also during winter and spring. Zooplankton were collected either in bulk (i.e. mixed species composition) or at one of 9 taxonomic levels: *Bosmina* spp., Calanoida, *Chaoborus* spp., Cladocera, Copepoda, Cyclopoida, *Daphnia* spp., *Eudiaptomus* spp., *Holopedium* spp. near the deepest point of each lake during the day or night (*Chaoborus* only) using vertical net tows. We also considered an allochthonous and autochthonous basal resource that was available for consumers in each site. These were leaf litter of the dominant terrestrial plants and pelagic phytoplankton, respectively. In some cases, we sampled soil OM or fresh leaves instead of litterfall. These were suitable alternatives because their isotopic ratios have been shown to be indistinguishable from both litterfall and dissolved OM inflowing into lakes (*7*, *54*). Phytoplankton were collected either by net tows during periods of high biomass (*8*, *11*, *21*), or isolated from particulate organic matter (POM) by their specific phospholipid fatty acids (*28*). However given the difficulty isolating pure phytoplankton using these two approaches, we inferred their isotopic signatures by sampling environmental water either on its own or with POM for

40% (n = 226) of the consumer observations. Environmental water was taken from the surface layer (ca. 0.5 m depth) and immediately filtered into airtight vials for later measurement of δ^2H. Subtracting the known discrimination by algae for δ^2H vs δ^1H [mean $\pm$ SD = -161.8 $\pm$ 23.0% across published studies (*28*, *61*); measured separately in Virginia lakes as (*11*): -195.6 $\pm$ 34.6%] from measurements of environmental water theoretically yielded δ^2H in phytoplankton. Where $\delta^{13}C$ and $\delta^{15}N$ values were desired, we also passed environmental water through cellulose filters with a nominal pore size of 0.8 μm to concentrate POM, which was back-rinsed into vials and dried and ground for isotope analysis. We then found the proportion of POM derived from terrestrial and pelagic resources with a two end member mixing model. Terrestrial δ^2H was measured while pelagic δ^2H was estimated from the known discrimination of phytoplankton for different isotopes in environmental water given δ^2H measured in water. The proportion of POM derived from each of the two resources and $\delta^{13}C$ and $\delta^{15}N$ measurements in terrestrial resources allowed us to solve a mixing model algebraically for $\delta^{13}C$ and $\delta^{15}N$ in phytoplankton (*6*, *54*). In 9 lakes, epiphytic algae were measured as autochthonous resources because they had indistinguishable δ^2H signatures from phytoplankton (*12*). All organic samples were dried and ground into a homogenous powder for isotopic analysis.

We also collected epilimnetic water samples across the sampling season at weekly to monthly intervals for 73% (n = 409) of the consumer observations. These were analysed for chlorophyll *a* using fluorometry, water colour (light absorbance at 440 nm) using spectrophotometry, and DOC, total nitrogen (TN), and total phosphorus (TP) using colorimetry. Values were averaged across the sampling period so as to be representative of overall conditions during the period of consumer growth. Full methods are described elsewhere (*6–9*, *11*, *16*, *21*, *23*, *28*, *62*).

Isotope Analysis

Stable isotope ratios of organic samples were measured on isotope-ratio mass spectrometers. Water samples were analysed for δ^2H on a cavity-ring-down laser spectrometer (*55*).

Geospatial Analysis

We delineated catchment boundaries for each lake by mapping flow direction and accumulation from digital elevation models. By then processing digital land use and cover datasets and satellite imagery through the total area that drained into a focal lake, we extracted catchment characteristics for each lake in a given sampling year. The characteristics included area of woody vegetation cover, mean vegetation density, mean soil carbon concentration (0-15 cm depth), lake area, lake perimeter, and soil wetness. Generally, catchment delineations and terrain analyses were at a 30 m resolution whereas landscape characterization and soil carbon estimates were at 250 and 1,000 m resolutions, respectively. This uniform approach ensured consistency in both resolution and data sources across lake districts. Our approach also produced very similar results to those derived from higher resolution catchment delineations provided by individual investigators and an alternative delineation that removed land intersecting other lakes upstream in the same catchment (full details given in Supplementary Methods S1).

Statistical Analysis

Hypothesis Testing with an Isotopic Mixing Model: We tested our five hypotheses by estimating terrestrial resource use (φ_T) within a Bayesian isotopic mixing model as a direct function of lake water chemistry, catchment characteristics, and consumer identity. Either a one- (δ^2H-only; n = 165), two- (δ^{13}C-δ^{15}N; n = 120), or three-isotope (δ^{13}C-δ^{15}N-δ^2H; n = 274) model was fitted depending on the number of isotopes measured for each consumer observation (total n = 559 separate observations). Briefly, the mixing model estimated the relative proportion of terrestrial and aquatic primary production used by each consumer type from stable isotope data and published physiological parameters that varied among consumers. By having only two potential resources, we could fit the exact same model to all observations irrespective of the number of isotopes measured; for a one isotope model only two

resources can be modelled because this reduces to only 1 unknown variable. Importantly, the absence of other resources did not bias estimation (Supplementary Methods S3). Additionally, for each consumer the model estimated a unique trophic position, trophic-level fractionation of N, and contribution of dietary water to δ^2H ratios from prior information (*7*, *28*, *42*; Supplementary Methods S2).

Our mixing model had the added benefit of sampling each estimate of terrestrial resource use from a distribution described by a hypothesised network of causal drivers representing our five focal hypotheses. In this network, we predicted allochthony from both the availability of allochthonous and autochthonous resources for the 409 observations with corresponding water chemistry values, allowing an increase in one resource to reduce the effect of the other (i.e. an interaction term). The availability of allochthonous resources was equal to the sum of DOC and POC that were terrestrially-derived. We had in-lake measurements of DOC that we multiplied against a model-estimated terrestrial proportion, but lacked such observations for POC. Therefore, we described the total terrestrial-derived POC as an estimated mean value across lakes that varied with observed catchment and within-lake variables. Using additional techniques for modelling latent variables, we further informed estimation of allochthonous resources, and hence terrestrial POC, by setting their values to be proportional to observed lake water colour. Water color was reported as absorbance at 440 nm, which is a strong indicator of terrestrially-derived humic substances (*63*). For autochthonous resources, their availability was equal to measured chlorophyll *a* concentrations. For the remaining 150 observations where no water chemistry was measured, we were still able to estimate terrestrial resource support as a function of consumer preference and season (Supplementary Methods S2). An additional benefit of our mixing model was that we could also incorporate uncertainty in source isotope data and dietary enrichment of δ^2H and trophic fractionation of δ^{15}N into estimates of resource use. Full details of the model are given in Supplementary Methods S2 with reproducible R code in Supplementary Data S2. Key abbreviations and symbols are listed in Table S3 in Supplementary Methods S2.

The model was fitted using Hamiltonian Monte Carlo sampling by calling RStan v2.8 from R v3.2, and we tested for convergence and model misspecification using standard approaches (Supplementary Methods S2). To infer effects, we calculated posterior means and 95% CIs for each parameter by drawing a subset of 1000 simulations. We did not reject hypotheses if 95% CIs for their associated effects excluded zero. All estimated coefficients were standardised to a common scale with a mean of 0 and SD of 1, so that we could compare the relative importance of different hypotheses.

Model Validation: The critical test of our mixing model is not only how well it fits our observations, but whether it can unbiasedly recover known parameters of simulated data, specifically consumer isotope ratios, φ_T, and the effect of lake and catchment-level characteristics on φ_T. We tested this in different scenarios by randomly sampling $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$ values for all 559 consumer observations in our empirical dataset from means and variances defining our mixing model in Supplementary Methods S2. First, we tested whether our ability to recover known values when each of seven potential sources of variation in the mixing model separately varied, as well as the prior means of dietary parameters. Second, we tested whether the model was robust to missing end members. Other resources, such as methane oxidising bacteria (MOB), certainly contribute to secondary production (*16*, *26*, *28*, *62*, *64*). Therefore, we simulated data with 10, 20, and 40% use of MOB, which had distinct isotopic signatures from terrestrial or pelagic resources (Supplementary Methods S3). A major strength of our approach was that it preserved structure in our original data, whilst exploring how different sources of variance impacted model performance.

H2: Supplementary Materials

Materials and Methods S1. Additional details for geospatial analyses

Materials and Methods S2. Additional details for statistical analysis

Materials and Methods S3. Validation and sensitivity of the Bayesian mixing model

Data file S1. Site-level summary of water quality and catchment characteristics for 147 lakes.

Data file S2. R code for stable isotope mixing model.

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H2: Acknowledgments

H3: Author contributions: The study was conceived by A. J. T. All authors collected the data. A. J. T., B. W. K., and G. M. W. analysed the data with input from all authors. A. J. T. wrote the manuscript with input from all authors

H3: Competing interests: The authors declare no competing interests.

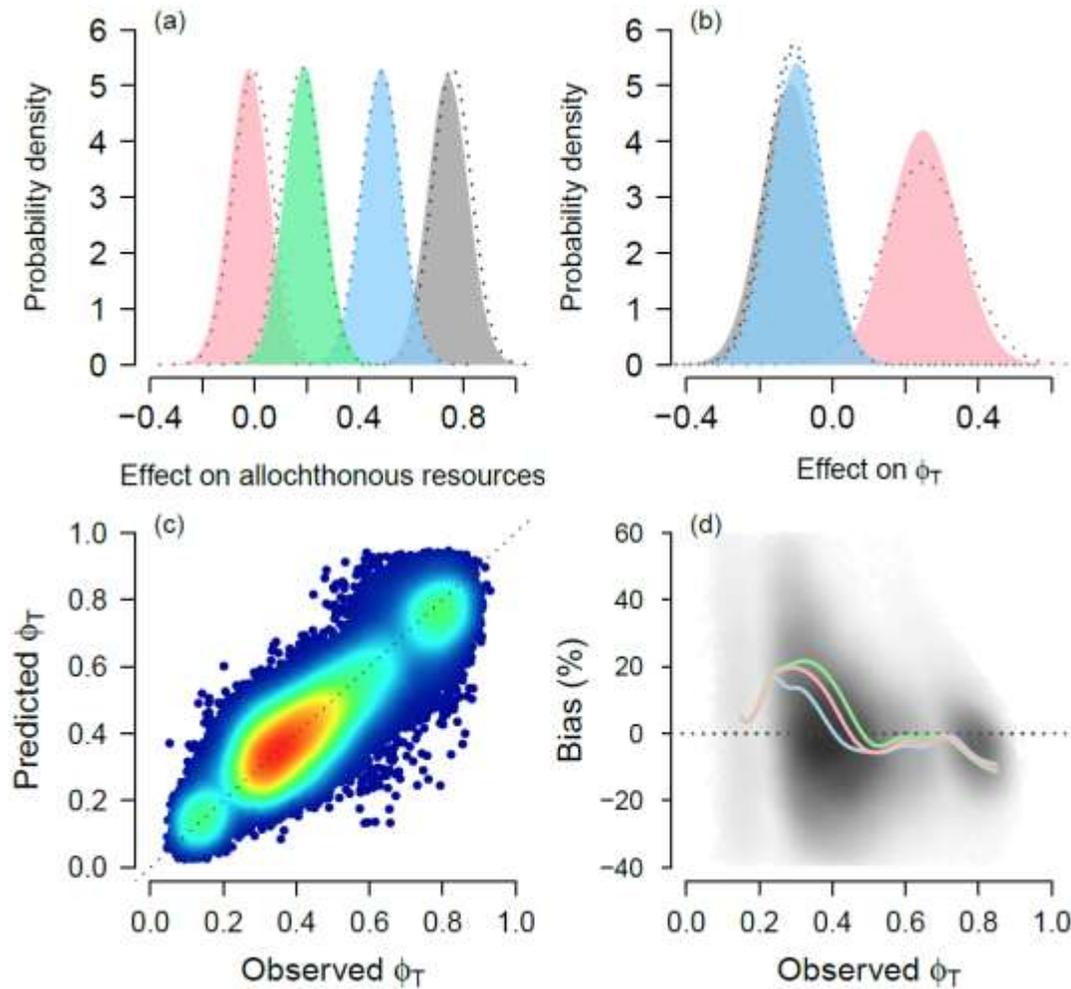**H3: Data and materials availability:** Data are available in Supplementary Materials.

Fig. **1**. **Model recovers known parameters across 100 simulated datasets that replicate our empirical observations**. Mean posterior distributions of the effects of: (**a**) DOC (gray), NDVI (pink), ratio of lake perimeter to area (blue), and area of woody vegetation per meter shoreline (green) on availability of allochthonous resources; (**b**) allochthonous resources (pink), lake chlorophyll *a* (gray), and an allochthonous resources × chlorophyll *a* interaction (blue) on terrestrial resource use (φ_T); dashed lines are known prior distributions. (**c**) Mean predicted versus observed (i.e. known) φ_T for 559 consumer observations in each of 100 simulations. Warmer colours indicate greater concentration of points (total $n = 55,900$). (**d**) Percent bias in mean predicted φ_T values. Darker shading indicates greater concentration of points. Lines are splines fitted through observations upon one (δ^2H-only, pink), two (δ^{13}C-δ^{15}N, green), or three (δ^{13}C-δ^{15}N-δ^2H, blue) isotopes.

Fig. 2. **Terrestrial resource (φ_T) use by lake zooplankton**. (**a**) Mean posterior estimate of φ_T for each of 559 consumer observations. (**b**) Scaled distributions of key catchment characteristics and unscaled means and SDs. (**c**) Focal lake regions ($n = 14$) superimposed on waterbodies at a 1-km resolution and a proxy of vegetation density (NDVI) at a 0.1° resolution in September 2015 (NASA Earth Observations data repository: http://neo.sci.gsfc.nasa.gov/).
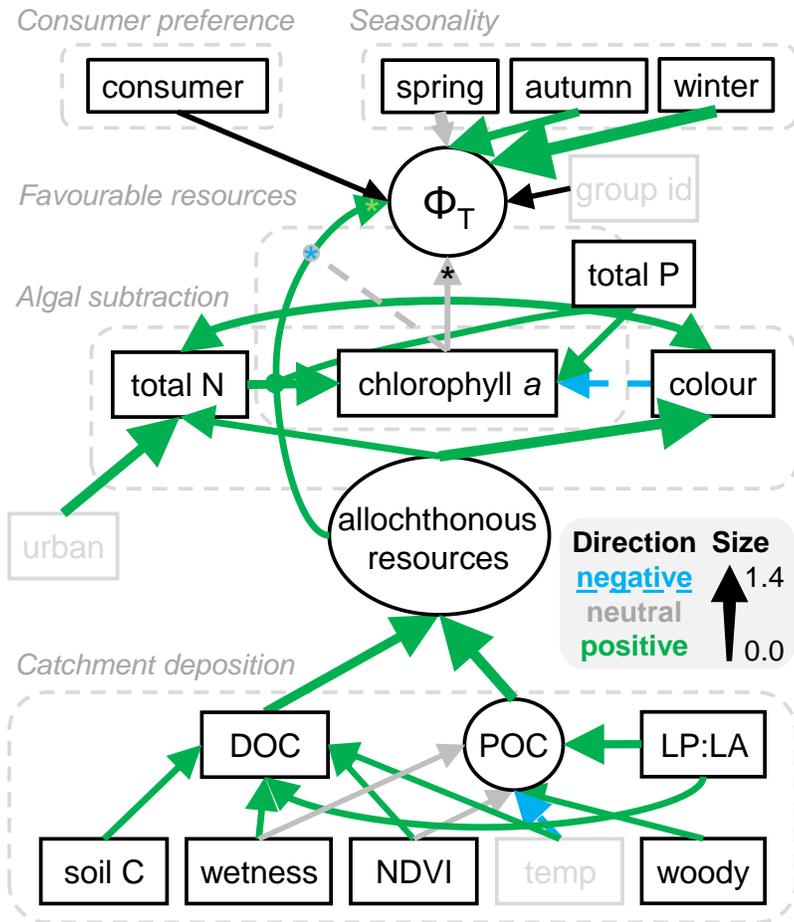
Fig. 3. **Modelled network of factors influencing terrestrial resource use (φ_T) by aquatic consumers across 147 lakes**. Arrows point at modelled variables, with mean effects of one variable on another proportional to standardised effect size (see legend). Lines ending in circles are interactions, * = random variation among consumers with colours showing direction of significant effects, black lines are intercepts with no 'effect direction', ellipses are unobserved (i.e. latent) variables, and grey boxes are covariates included to explain better the connections between modelled variables and predictors of interest. Five mechanisms explaining variation in φ_T are associated with broken boxes. NDVI = vegetation density; temp = mean monthly temperature of warmest quarter; woody = area of woody vegetation in catchment per meter shoreline; LP:LA = ratio of lake perimeter to area; group id = research group that collected the data, e.g. accounting for variation in sampling. Bayesian R^2 for consumers with one (δ^2H-only), two (δ^{13}C-δ^{15}N), or three (δ^{13}C-δ^{15}N-δ^2H) observed isotopes were = 0.64, 0.98, and 0.99, respectively (Fig. S2 in Supplementary Methods S2).

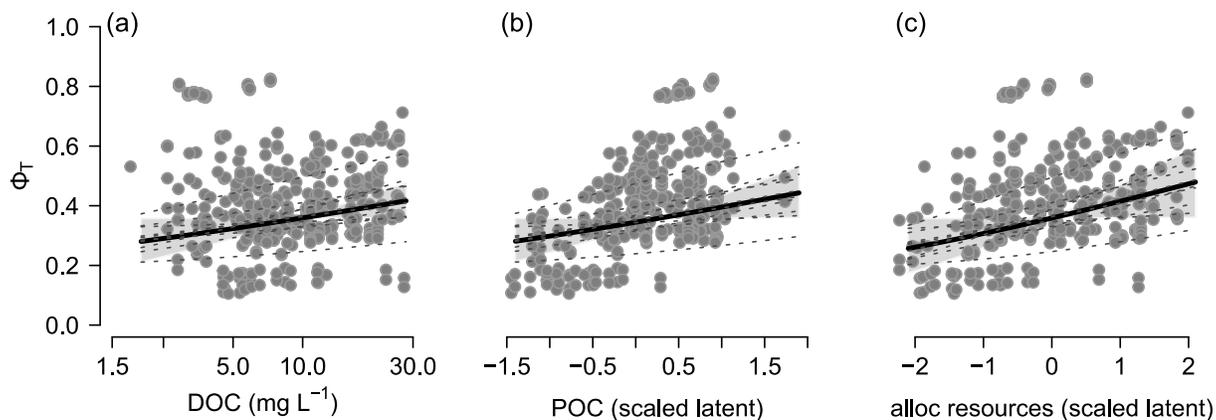**Fig**. 4. φ_T **increases with the estimated availability of (a) DOC, (b) POC, and (c) their summed contribution towards allochthonous (alloc) resources**. Points are mean estimated φ_T for each of 409 consumer observations with corresponding water chemistry measurements. Solid line is the mean increase across all consumers at mean levels of all other water chemistry variables, with shaded polygon denoting 95% CI and dotted lines denoting consumer-specific responses.
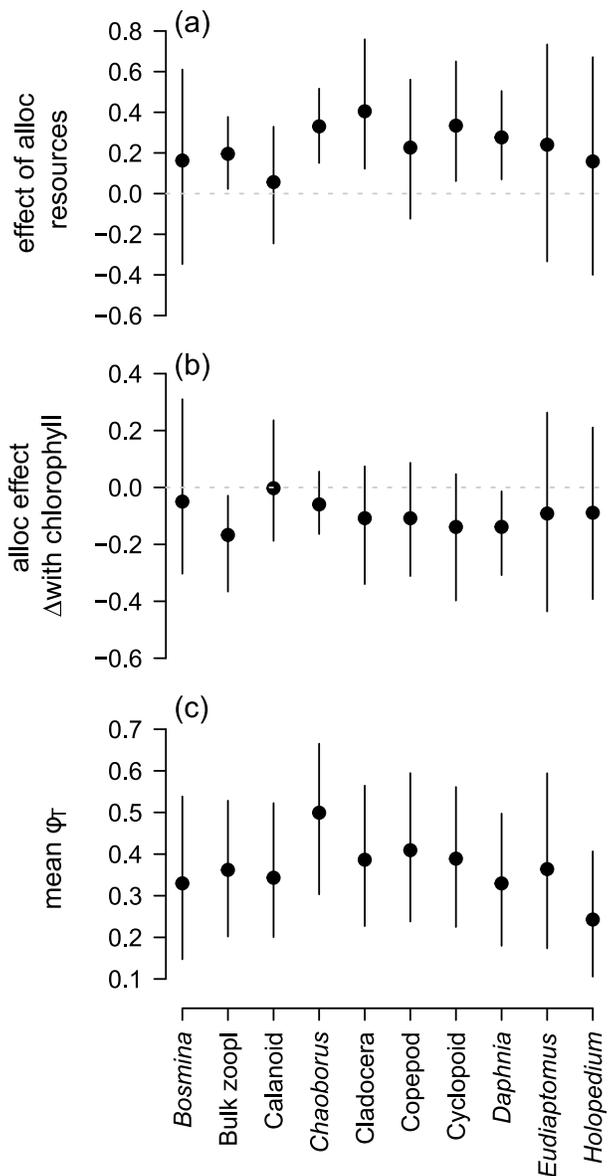
Fig. **5**. **Consumer-specific variation in φ_{T}.** Mean ± 95% CIs plotted for (**a**) effect of allochthonous

(alloc) resources on φ_{T}; (**b**) change in effect of allochthonous resources on φ_{T} with increasing lake water

chlorophyll *a*; and (**c**) φ_{T} at mean water chemistry levels across sites.