

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
- One-sentence summary: Widespread evidence that aquatic consumers use terrestrial resources depending on the features of surrounding catchments.

H2:Authors

Andrew J. Tanentzap,^{1*} Brian W. Kielstra,² Grace M. Wilkinson,³ Martin Berggren,⁴ Nicola Craig,⁵ Paul A. del Giorgio,⁶ Jonathan Grey,⁷ John M. Gunn,⁸ Stuart E. Jones,⁹ Jan Karlsson,¹⁰ Christopher T. Solomon,¹¹ Michael L. Pace³

H2:Affiliations

¹Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, Cambridge, CB2 3EA, UK.

²Department of Forest & Conservation Sciences, University of British Columbia, Vancouver, BC Canada V6T 1Z4.

³Department of Environmental Sciences, University of Virginia, Charlottesville, VA USA 22904.

⁴Department of Physical Geography and Ecosystem Science, Lund University, S-223 62 Lund, Sweden.

⁵Department of Natural Resource Sciences, McGill University, Ste. Anne de Bellevue, QC, Canada H9X 3V9.

⁶Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC, Canada H3C 3P8.

⁷Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK.

⁸Living With Lakes Centre, Laurentian University, Sudbury, ON Canada P3E 6H5.

⁹Department of Biological Sciences, University of Notre Dame, Notre Dame, IN USA 46556.

¹⁰Climate Impacts Research Centre (CIRC), Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden.

¹¹Cary Institute of Ecosystem Studies, Millbrook, NY USA 12545

*Author for correspondence: ajt65@cam.ac.uk.

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 ($\delta^2\text{H}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) 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

93 in allochthony reported to date. As our study sites were a non-random collection of lakes for which
94 terrestrial resources were likely more important, on average, than elsewhere, we focused on
95 understanding when, and for which consumers, allochthony was high in our subset of global lake types.
96 We do so by simultaneously testing five mutually-inclusive hypotheses around cross-ecosystem
97 resources and comparing their relative support:

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

100 *Catchment deposition hypothesis:* Allochthony increases as more t-OM is exported from the
101 surrounding catchment. A greater quantity and reactivity of t-OM can be made available for
102 consumption by consumers at the base of aquatic food webs as the coverage and density of labile
103 vegetation and soil carbon in the surrounding catchment increase (9, 36). A larger land-water interface
104 can also increase the geomorphic potential of catchments to deliver t-OM into receiving food webs (14,
105 37).

106 *Algal subtraction hypothesis:* Allochthony increases with the availability of t-OM where algal
107 production becomes limited by shading more than it benefits from the nutrients associated with t-OM
108 (38).

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

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

114 Our analysis is the first large-scale effort explicitly linking resource use by aquatic organisms to
115 catchment characteristics such as land cover. We collated stable isotope ($\delta^2\text{H}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$)
116 measurements taken year-round for 559 observations of pelagic consumers across 147 lakes in many of

as compared with within-lake resources (fig. S1). Pelagic phytoplankton, for which isotopic signatures were directly measured for $n = 333$ consumer observations and estimated in another $n = 226$ from their photosynthetic $\delta^2\text{H}$ discrimination, varied much more in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than terrestrial resources, with no clear difference between either the measured or estimated values (fig. S1). 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). Additional simulations showed that all focal parameters were relatively insensitive to increased uncertainty in other sources, such as the isotope measurements themselves (fig. S2), biased prior information about consumer physiology (fig. S3), and potentially missing resources that would bias determination of the within-lake resources, such as methane oxidising bacteria (fig. S4).

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 file 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. S5). 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. S6), 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 calanoid copepods, 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). All other parameter estimates are reported in table S1.

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 suggest that t-OM 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 cyclopoid copepods 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 use 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

We found that estimates of terrestrial resource use were positively biased by an average of up to 18% on a relative basis (ca. 7% 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. S10). 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. S10), 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 when evaluating 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 (15, 34–35), though without rigorous statistical tests. 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 ^2H relative to ^1H 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 $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values of fresh leaves 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 $\delta^2\text{H}$ 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.

332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355

333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355

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 $\delta^2\text{H}$. Subtracting the known discrimination by algae against ^2H relative to ^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 $\delta^2\text{H}$ in phytoplankton. Where $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were desired, we also passed environmental water through cellulose filters with a nominal pore size of $0.8\ \mu\text{m}$ to concentrate POM, which was back-rinsed into vials and dried and ground for isotope analysis. We then estimated the proportion of POM derived from terrestrial and pelagic resources with a two end member mixing model. Terrestrial $\delta^2\text{H}$ was measured while pelagic $\delta^2\text{H}$ was estimated from the known

discrimination of phytoplankton for different isotopes in environmental water given $\delta^2\text{H}$ measured in water. The proportion of POM derived from each of the two resources and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements in terrestrial resources allowed us to solve a mixing model algebraically for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in phytoplankton (6, 54). In 9 lakes, epiphytic algae were measured as autochthonous resources because they had indistinguishable $\delta^2\text{H}$ 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 $\delta^2\text{H}$ 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 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- ($\delta^2\text{H}$ -only; $n = 165$), two- ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$; $n = 120$), or three-isotope ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ - $\delta^2\text{H}$; $n = 274$) 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 $\delta^2\text{H}$ 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 $\delta^2\text{H}$ and trophic fractionation of $\delta^{15}\text{N}$ into estimates of resource use. Full details of the model are given in supplementary methods S2 with reproducible R code in supplementary data file S2. Key abbreviations and symbols are listed in table 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 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ 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

supplementary methods S1. Additional details for geospatial analyses.

supplementary methods S2. Additional details for statistical analysis.

supplementary methods S3. Validation and sensitivity of the Bayesian mixing model.

fig. S1. End members used in mixing model and corresponding with each of 559 consumer observations.

fig. S2. Sensitivity of BMM to changes in 7 SDs.

fig. S3. Sensitivity of BMM to misinformed dietary priors.

fig. S4. Model recovers known parameters despite not accounting for datasets with consumer use of MOB.

fig. S5. Predicted versus observed isotope ratios for 559 consumer observations.

fig. S6. Prior (light grey curves) and posterior (dark gray curves) of φ_T for each of 559 observations organised by consumer type.

fig. S7. Lake area distributions globally (black lines) and within our dataset (blue lines).

fig. S8. Dissolved organic carbon (DOC) distributions from 7,514 worldwide lakes.

fig. S9. Chlorophyll *a* distribution from 80,012 worldwide lakes.

fig. S10. Model recovers known parameters across 100 simulated datasets that span the range of φ_T (i.e. 0 – 1).

fig. S11. Catchment area estimated for 147 lakes in our isotope dataset.

fig. S12. Proportion of each catchment covered with one of four woody vegetation types.

fig. S13. Vegetation, geomorphology, and soil characteristics.

fig. S14. Catchment area for 46 lakes.

fig. S15. Percent overlap in catchments of each of 46 lakes delineated with three different approaches.

fig. S16. Model recovers known parameters despite random noise around the mean effects of covariates predicting the availability of allochthonous resources ζ_{kl} .

fig. S17. Alternate ways of modelling terrestrial organic matter deposition.

table S1. Mean and 95% CIs for model parameter estimates associated with eqns S1-S11.

table S2. Key symbols and abbreviations used in the Main Text and Supplementary Methods.

table S3. Reclassification of 2005 North America Landcover.

table S4. Reclassification of 2006 European Land Cover.

table S5. Consumer specific dietary parameters.

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.

H2: References and Notes

1. G. A. Polis, W. B. Anderson, R. D. Holt, Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Evol. Syst.* **28**, 289–316 (1997).
2. P. Bartels *et al.*, Terrestrial subsidies to lake food webs: an experimental approach. *Oecologia* **168**, 807–818 (2011).
3. J. Grey, R. I. Jones, D. Sleep, Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnol. Oceanogr.* **46**, 505–513 (2001).
4. M. L. Pace *et al.*, Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* **427**, 240–243 (2004).
5. S. R. Carpenter *et al.*, Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology* **86**, 2737–2750 (2005).
6. J. J. Cole *et al.*, Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 1975–1980 (2011).
7. C. T. Solomon *et al.*, Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. *Ecology* **92**, 1115–1125 (2011).
8. G. M. Wilkinson, S. R. Carpenter, J. J. Cole, M. L. Pace, C. Yang, Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. *Freshw. Biol.* **58**, 2037–2049 (2013).
9. A. J. Tanentzap *et al.*, Forests fuel fish growth in freshwater deltas. *Nat. Commun.* **5**, 4077 (2014).
10. N. Craig, S. E. Jones, B. C. Weidel, C. T. Solomon, Habitat, not resource availability, limits consumer production in lake ecosystems. *Limnol. Oceanogr.* **60**, 2079–2089 (2015).
11. K. A. Emery, G. M. Wilkinson, F. G. Ballard, M. L. Pace, Use of allochthonous resources by zooplankton in reservoirs. *Hydrobiologia* **758**, 257–269 (2015).

- 499 12. J. Karlsson *et al.*, Terrestrial organic matter support of lake food webs: Evidence from lake
500 metabolism and stable hydrogen isotopes of consumers. *Limnol. Oceanogr.* **57**, 1042–1048 (2012).
- 501 13. T. Mehner *et al.*, Weak response of animal allochthony and production to enhanced supply of
502 terrestrial leaf litter in nutrient-rich lakes. *Ecosystems* **19**, 311–325 (2015).
- 503 14. A. L. Babler, A. Pilati, M. J. Vanni, Terrestrial support of detritivorous fish populations decreases
504 with watershed size. *Ecosphere* **2**, 1–23 (2011).
- 505 15. M. T. Brett, M. J. Kainz, S. J. Taipale, H. Seshan, Phytoplankton, not allochthonous carbon,
506 sustains herbivorous zooplankton production. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 21197–21201
507 (2009).
- 508 16. P. T. Kelly, C. T. Solomon, B. C. Weidel, S. E. Jones, Terrestrial carbon is a resource, but not a
509 subsidy, for lake zooplankton. *Ecology* **95**, 1236–1242 (2014).
- 510 17. J. J. Cole *et al.*, Differential support of lake food webs by three types of terrestrial organic carbon.
511 *Ecol. Lett.* **9**, 558–568 (2006).
- 512 18. M. Berggren *et al.*, Lake secondary production fueled by rapid transfer of low molecular weight
513 organic carbon from terrestrial sources to aquatic consumers. *Ecol. Lett.* **13**, 870–880 (2010).
- 514 19. B. C. McMeans, A.-M. Koussoroplis, M. T. Arts, M. J. Kainz, Terrestrial dissolved organic matter
515 supports growth and reproduction of *Daphnia magna* when algae are limiting. *J. Plankton Res.* **37**,
516 1201–1209 (2015).
- 517 20. S. J. Taipale *et al.*, Differing *Daphnia magna* assimilation efficiencies for terrestrial, bacterial, and
518 algal carbon and fatty acids. *Ecology* **95**, 563–576 (2014).
- 519 21. J. Grey, R. I. Jones, D. Sleep, Stable isotope analysis of the origins of zooplankton carbon in lakes
520 of differing trophic state. *Oecologia* **123**, 232–240.
- 521 22. J. Karlsson *et al.*, Light limitation of nutrient-poor lake ecosystems. *Nature* **460**, 506–509 (2009).

23. J. Karlsson *et al.*, Terrestrial organic matter input suppresses biomass production in lake ecosystems. *Ecology* **96**, 2870–2876 (2015).
24. S. R. Carpenter, J. J. Cole, M. L. Pace, G. M. Wilkinson, Response of plankton to nutrients, planktivory and terrestrial organic matter: a model analysis of whole-lake experiments. *Ecol. Lett.* **19**, 230–239 (2016).
25. T. B. Francis *et al.*, Habitat structure determines resource use by zooplankton in temperate lakes. *Ecol. Lett.* **14**, 364–372 (2011).
26. D. C. P. Lau, I. Sundh, T. Vrede, J. Pickova, W. Goedkoop, Autochthonous resources are the main driver of consumer production in dystrophic boreal lakes. *Ecology* **95**, 1506–1519 (2014).
27. A. W. E. Galloway *et al.*, Diet-specific biomarkers show that high-quality phytoplankton fuels herbivorous zooplankton in large boreal lakes. *Freshw. Biol.* **59**, 1902–1915 (2014).
28. M. Berggren, S. E. Ziegler, N. F. St-Gelais, B. E. Beisner, P. A. del Giorgio, Contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes. *Ecology* **95**, 1947–1959 (2014).
29. K. C. Rose, C. E. Williamson, C. E. H. Kissman, J. E. Saros, Does allochthony in lakes change across an elevation gradient? *Ecology* **96**, 3281–3291 (2015).
30. M. L. Cadenasso, S. T. A. Pickett, K. C. Weathers, C. G. Jones, A Framework for a Theory of Ecological Boundaries. *BioScience* **53**, 750–758 (2003).
31. L. B. Marczak, R. M. Thompson, J. S. Richardson, Meta-Analysis: Trophic Level, Habitat, and Productivity Shape the Food Web Effects of Resource Subsidies. *Ecology* **88**, 140–148 (2007).
32. S. J. Leroux, M. Loreau, Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecol. Lett.* **11**, 1147–1156 (2008).
33. B. C. McMeans, K. S. McCann, M. Humphries, N. Rooney, A. T. Fisk, Food web structure in temporally-forced ecosystems. *Trends Ecol. Evol.* **30**, 662–672 (2015).

34. B. Fry, Alternative approaches for solving underdetermined isotope mixing problems. *Mar. Ecol. Prog. Ser.* **472**, 1–13 (2013).
35. M. T. Brett, Resource polygon geometry predicts Bayesian stable isotope mixing model bias. *Mar. Ecol. Prog. Ser.* **514**, 1–12 (2014).
36. D. N. Kothawala et al., Controls of dissolved organic matter quality: evidence from a large-scale boreal lake survey. *Glob. Change Biol.* **20**, 1101–1114 (2014).
37. P. Kortelainen, Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. *Can. J. Fish. Aquat. Sci.* **50**, 1477–1483 (1993).
38. S. E. Jones, C. T. Solomon, B. C. Weidel, Subsidy or subtraction: how do terrestrial inputs influence consumer production in lakes? *Freshwater Reviews.* **5**, 37–49 (2012).
39. J. Karlsson, A. Jonsson, M. Meili, M. Jansson, $\delta^{15}\text{N}$ of zooplankton species in subarctic lakes in northern Sweden: effects of diet and trophic fractionation. *Freshw. Biol.* **49**, 526–534 (2004).
40. M. Berggren, A.-K. Bergström, J. Karlsson, Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and Fall. *PLoS ONE* **10**, e0120575 (2015).
41. B. Matthews, A. Mazumder, Habitat specialization and the exploitation of allochthonous carbon by zooplankton. *Ecology* **87**, 2800–2812 (2006).
42. G. M. Wilkinson, J. J. Cole, M. L. Pace, Deuterium as a food source tracer: Sensitivity to environmental water, lipid content, and hydrogen exchange. *Limnol. Oceanogr. Methods* **13**, 213–223 (2015).
43. M. A. Xenopoulos et al., Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the Upper Great Lakes region and selected regions globally. *Limnol. Oceanogr.* **48**, 2321–2334 (2003).

- 569 44. R. D. Batt *et al.*, Altered energy flow in the food web of an experimentally darkened lake.
570 *Ecosphere* **6**, 1–23 (2015).
- 571 45. J. A. Zwart *et al.*, Metabolic and physiochemical responses to a whole-lake experimental increase in
572 dissolved organic carbon in a north-temperate lake. *Limnol. Oceanogr.* **61**, 723–734 (2016).
- 573 46. A. D. Persaud, P. J. Dillon, D. Lasenby, N. D. Yan, Stable isotope variability of meso-zooplankton
574 along a gradient of dissolved organic carbon. *Freshw. Biol.* **54**, 1705–1719 (2009).
- 575 47. A. D. Persaud, P. J. Dillon, Differences in zooplankton feeding rates and isotopic signatures from
576 three temperate lakes. *Aquat. Sci.* **73**, 261–273 (2010).
- 577 48. P. C. Hanson, S. R. Carpenter, J. A. Cardille, M. T. Coe, L. A. Winslow, Small lakes dominate a
578 random sample of regional lake characteristics. *Freshw. Biol.* **52**, 814–822 (2007).
- 579 49. M. E. Palmer, N. D. Yan, A. M. Paterson, R. E. Girard, Water quality changes in south-central
580 Ontario lakes and the role of local factors in regulating lake response to regional stressors. *Can. J.*
581 *Fish. Aquat. Sci.* **68**, 1038–1050 (2011).
- 582 50. J. A. Downing *et al.*, The global abundance and size distribution of lakes, ponds, and
583 impoundments. *Limnol. Oceanogr.* **51**, 2388–2397 (2006).
- 584 51. S. Sobek, L. J. Tranvik, Y. T. Prairie, P. Kortelainen, J. J. Cole, Patterns and regulation of dissolved
585 organic carbon: An analysis of 7,500 widely distributed lakes. *Limnol. Oceanogr.* **52**, 1208–1219
586 (2007).
- 587 52. M. J. Sayers *et al.*, A new method to generate a high-resolution global distribution map of lake
588 chlorophyll. *Int. J. Remote Sens.* **36**, 1942–1964 (2015).
- 589 53. G. M. Wilkinson, S. R. Carpenter, J. J. Cole, M. L. Pace, Use of deep autochthonous resources by
590 zooplankton: results of a metalimnetic addition of ^{13}C to a small lake. *Limnol. Oceanogr.* **59**, 986–
591 996 (2014).

54. C. Yang, G. M. Wilkinson, J. J. Cole, S. A. Macko, M. L. Pace, Assigning hydrogen, carbon, and nitrogen isotope values for phytoplankton and terrestrial detritus in aquatic food web studies. *Inland Waters* **4**, 233–242 (2014).
55. R. R. Doucett, J. C. Marks, D. W. Blinn, M. Caron, B. A. Hungate, Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. *Ecology* **88**, 1587–1592 (2007).
56. S. C. Zeug, K. O. Winemiller, Evidence supporting the importance of terrestrial carbon in a large-river food web. *Ecology* **89**, 1733–1743 (2008).
57. L. B. Marczak *et al.*, Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecol. Appl.* **20**, 126–134 (2010).
58. S. R. Carpenter *et al.*, Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol. Monogr.* **71**, 163–186 (2001).
59. D. W. Schindler, P. G. Lee, Comprehensive conservation planning to protect biodiversity and ecosystem services in Canadian boreal regions under a warming climate and increasing exploitation. *Biol. Conserv.* **143**, 1571–1586 (2010).
60. M. C. Hansen *et al.*, High-resolution global maps of 21st-century forest cover change. *Science*. **342**, 850–853 (2013).
61. K. L. Hondula, M. L. Pace, J. J. Cole, R. D. Batt, Hydrogen isotope discrimination in aquatic primary producers: implications for aquatic food web studies. *Aquat Sci.* **76**, 217–229 (2013).
62. R. I. Jones, J. Grey, D. Sleep, L. Arvola, Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* **86**, 97–104 (1999).
63. I. D. Cuthbert, P. del Giorgio, Toward a standard method of measuring color in freshwater *Limnol. Oceanogr.* **37**, 1319–1326 (1992).
64. J. Grey, The incredible lightness of being methane-fuelled: stable isotopes reveal alternative energy pathways in aquatic ecosystems and beyond. *Front. Ecol. Evol.*, **4**, 8 (2016).

65. T. G. Farr *et al.*, The Shuttle Radar Topography Mission. *Rev. Geophys.* **45**, RG2004 (2007).
66. NASA Jet Propulsion Laboratory, NASA Shuttle Radar Topography Mission United States 1 arc second. Version 3. NASA EOSDIS Land Processes DAAC. *USGS Earth Resources Observation and Science Center*. <http://dx.doi.org/10.5067/MEaSURES/SRTM/SRTMUS1.003> (2013).
67. European Environment Agency, EU-DEM (2013). Available at: http://www.eea.europa.eu/data-and-maps/data/ds_resolveuid/ca503256de1b4231b029e4145d0a8b7b.
68. QGIS Development Team, QGIS Geographic Information System. *Open Source Geospatial Foundation Project* (2015). Available at: <http://qgis.osgeo.org>.
69. Commission for Environmental Cooperation, North American Atlas Lakes, 2009. *Natural Resources Canada/Canadian Center for Remote Sensing, United States Geological Survey; Instituto Nacional de Estadística y Geografía, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and Comisión Nacional Forestal* (2011). Available at: <http://www.cec.org/Page.asp?PageID=122&ContentID=2310&SiteNodeID=497>.
70. Commission for Environmental Cooperation, North American Land Cover at 250 m spatial resolution. *Natural Resources Canada/Canadian Center for Remote Sensing, United States Geological Survey, Instituto Nacional de Estadística y Geografía, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and Comisión Nacional Forestal* (2005). Available at: <http://www.cec.org/Page.asp?PageID=924&ContentID=2819>.
71. European Environment Agency, Corine Land Cover 2006 raster data version 17 (2014). Available at: <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3>.
72. Land Processes Distributed Active Archive Center, MOD13Q1 version 005. *NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science* (2014). Available at: https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1.

73. ISRIC – World Soil Information, SoilGrids: an automated system for global soil mapping (2013).
Available at: <http://soilgrids1km.isric.org>
74. T. Hengl *et al.*, SoilGrids1km — Global soil information based on automated mapping. *PLoS ONE* **9**, e105992 (2014).
75. R. J. Hijmans, S. E., Cameron, J. L., Parra, P. G., Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
76. J. B. Lindsay, The Whitebox Geospatial Analysis Tools project and open-access GIS. Proceedings of the GIS Research UK 22nd Annual Conference, The University of Glasgow, 16-18 April, 2014 (2014).
77. I. D. Moore, R. B. Grayson, A. R. Ladson, Digital terrain modelling: A review of hydrological, geomorphological, and biological applications. *Hydrol. Process.* **5**, 3–30 (1991).
78. B. Lehner, P. Döll, Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* **296**, 1–22 (2004).
79. C. T. Solomon *et al.*, The influence of environmental water on the hydrogen stable isotope ratio in aquatic consumers. *Oecologia* **161**, 313–324 (2009).
80. M. A. Vanderklift, S. Ponsard, Sources of variation in consumer-diet delta 15N enrichment: a meta-analysis. *Oecologia* **136**, 169–182 (2003).
81. J. R. Taylor, *An introduction to error analysis: the study of uncertainties in physical measurements* (University Science Books, Sausalito, 1997).
82. Shipley, B. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference* (Cambridge University Press, Cambridge, 2000)
83. A. J. Tanentzap *et al.*, Identifying pathways for managing multiple disturbances to limit plant invasions. *J. Appl. Ecol.* **51**, 1015–1023 (2014).

84. G. A. Weyhenmeyer, J. Karlsson, Nonlinear response of dissolved organic carbon concentrations in boreal lakes to increasing temperatures. *Limnol. Oceanogr.* **54**, 2513–2519 (2009).
85. I. F. Creed, S. E. Sanford, F. D. Beall, L. A. Molot, P. J. Dillon, Cryptic wetlands: integrating hidden wetlands in regression models of the export of dissolved organic carbon from forested landscapes. *Hydrol. Process.* **17**, 3629–3648 (2003).
86. C. Gudas et al., Temperature-controlled organic carbon mineralization in lake sediments. *Nature* **466**, 478–481 (2010).
87. A. Gelman et al., *Bayesian data analysis, third edition* (Chapman and Hall/CRC, Boca Raton, 2013).
88. D. Lewandowski, D. Kurowicka, H. Joe, Generating random correlation matrices based on vines and extended onion method. *J. Multivar. Anal.* **100**, 1989–2001 (2009).
89. J. B. Grace et al., Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* **3**, 1–44 (2012).
90. P. Kankaala et al., Experimental $\delta^{13}\text{C}$ evidence for a contribution of methane to pelagic food webs in lakes. *Limnol. Oceanogr.* **51**, 2821–2827 (2006).
91. D. R. Engstrom, Influence of vegetation and hydrology on the humus budgets of Labrador lakes. *Can. J. Fish. Aquat. Sci.* **44**, 1306–1314 (1987).
92. L. B. Knoll, M. J. Vanni, W. H. Renwick, S. Kollie, Burial rates and stoichiometry of sedimentary carbon, nitrogen and phosphorus in Midwestern US reservoirs. *Freshw Biol.* **59**, 2342–2353 (2014).
93. S. E. Gergel, M. G. Turner, T. K. Kratz, Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers. *Ecol. Appl.* **9**, 1377–1390 (1999).
94. C. D. Canham et al., A spatially explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes. *Ecol. Appl.* **14**, 839–854 (2004).

686

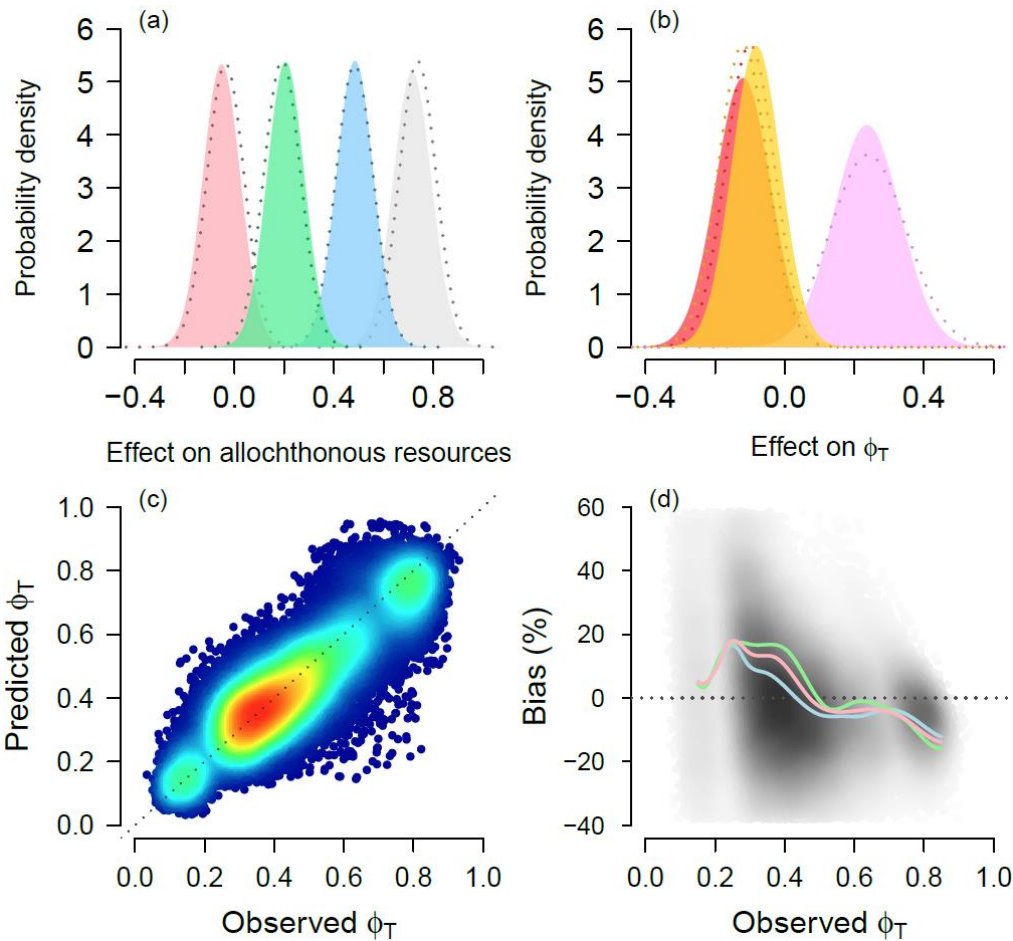
687

690

694

697

698



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

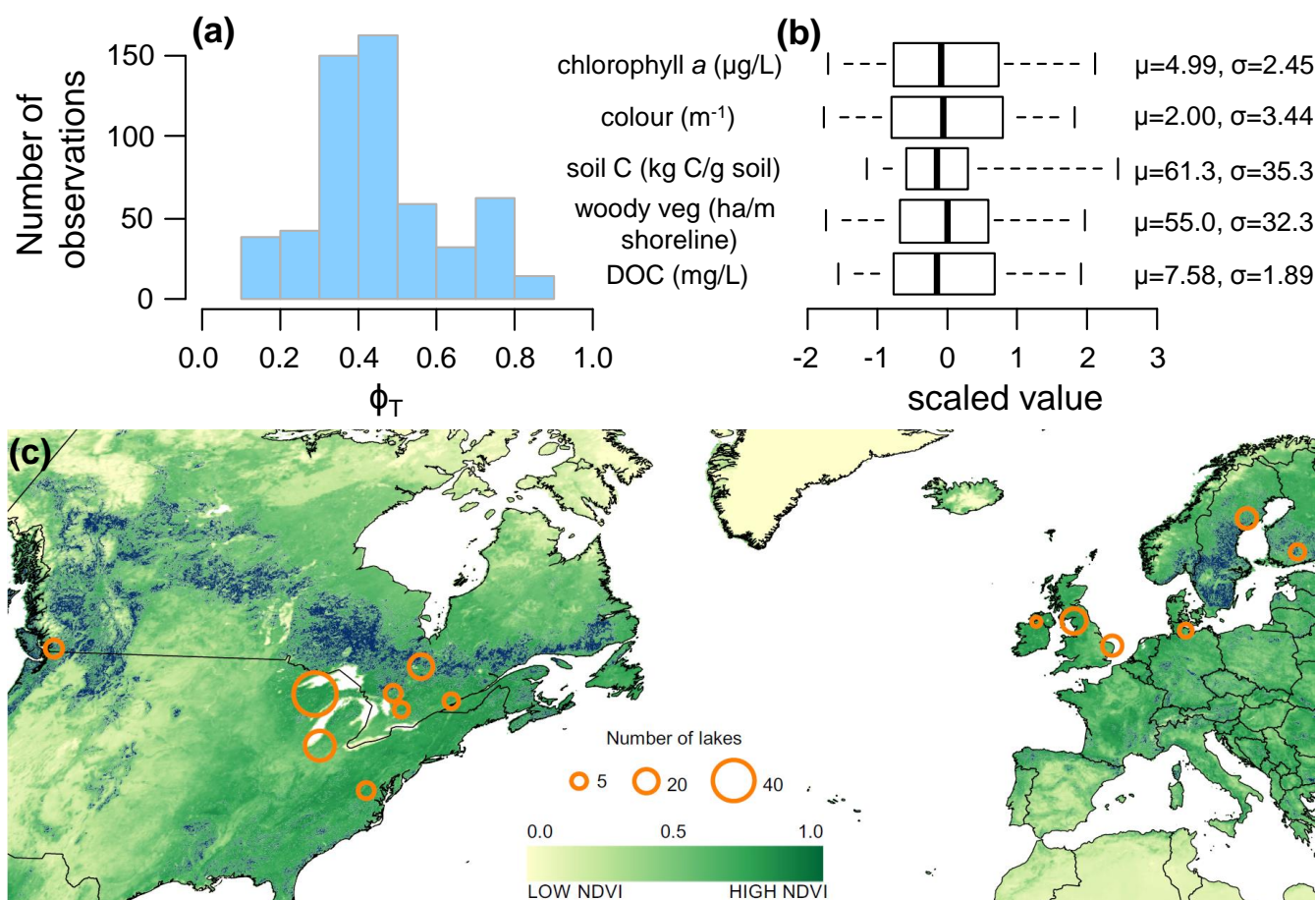


Fig. 2. Terrestrial resource (ϕ_T) use by lake zooplankton. (a) Mean posterior estimate of ϕ_T for each of 559 consumer observations. (b) Scaled distributions of key catchment characteristics and unscaled means and SDs. (c) Focal lake regions ($n = 14$) superimposed on waterbodies at a 1-km resolution 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/>).

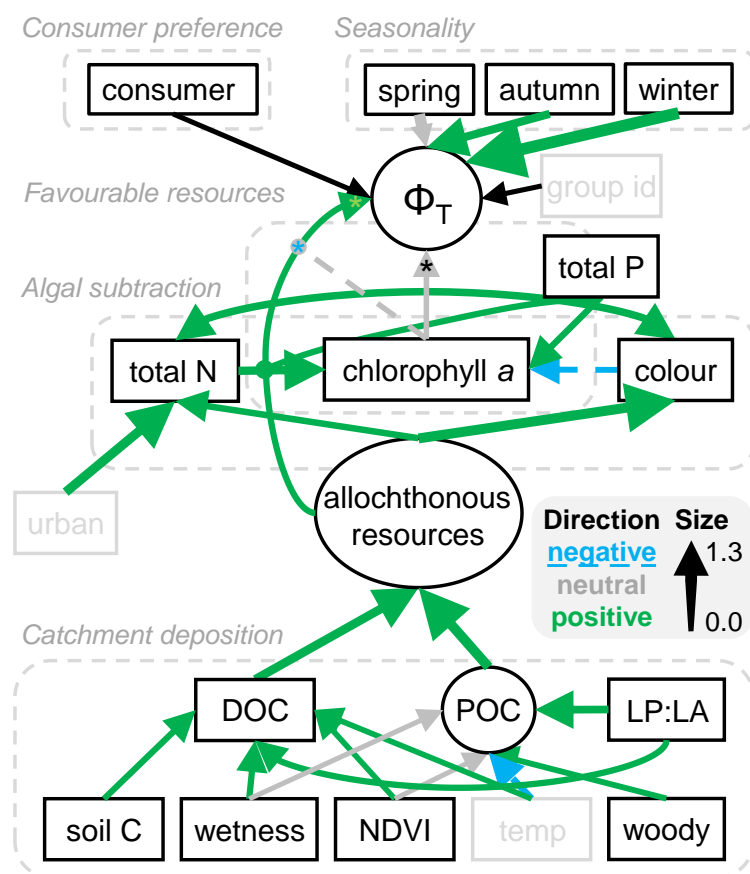


Fig. 3. Modelled network of factors influencing terrestrial resource use (ϕ_T) by aquatic consumers across 147 lakes. Arrows point at modelled variables, with mean effects of one variable on another proportional to standardised effect size (see legend). Lines ending in circles are interactions, * = random 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 ($\delta^2\text{H}$ -only), two ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$), or three ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ - $\delta^2\text{H}$) observed isotopes were = 0.64, 0.98, and 0.99, respectively (fig. S5).

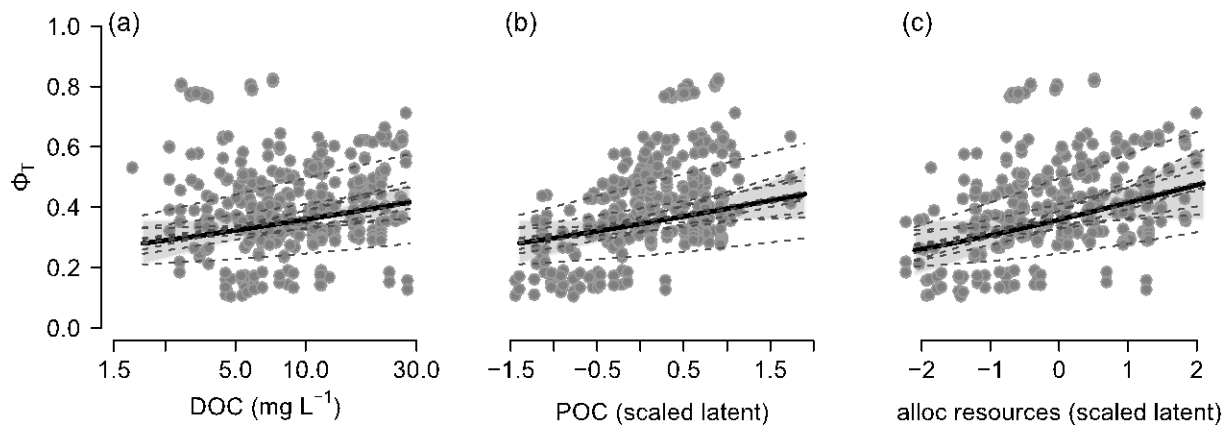


Fig. 4. ϕ_T increases with the estimated availability of (a) DOC, (b) POC, and (c) their summed contribution towards allochthonous (alloc) resources. Points are mean estimated ϕ_T for each of 409 consumer observations with corresponding water chemistry measurements. Solid line is the mean increase across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

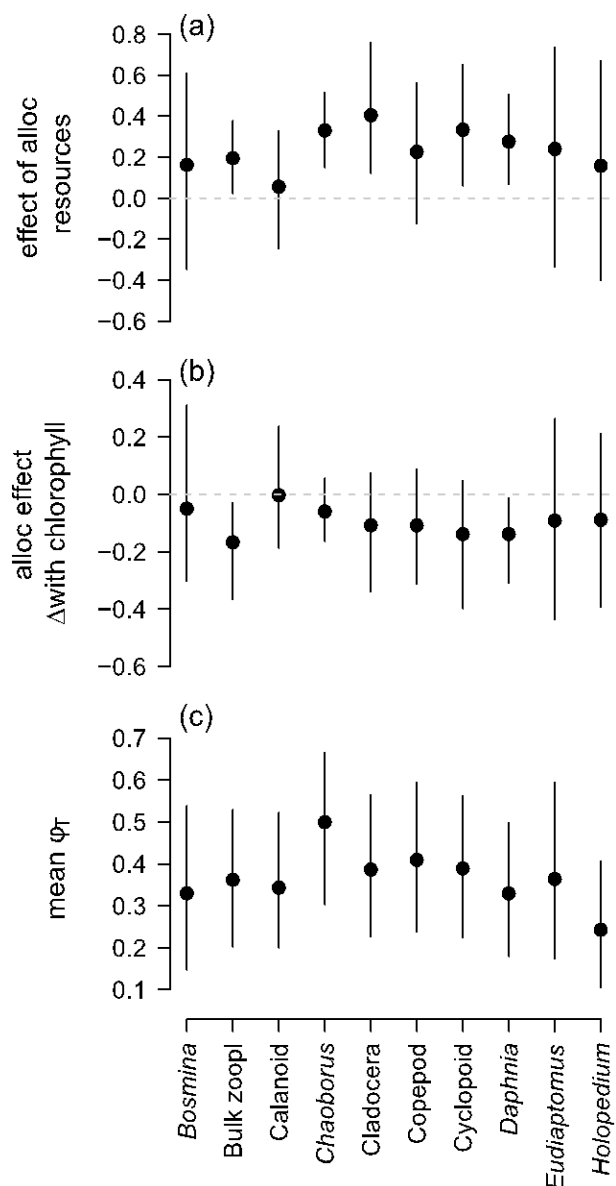


Fig. 5. Consumer-specific variation in ϕ_T . Mean \pm 95% CIs plotted for (a) effect of allochthonous (alloc) resources on ϕ_T ; (b) change in effect of allochthonous resources on ϕ_T with increasing lake water chlorophyll *a*; and (c) ϕ_T at mean water chemistry levels across sites.