

OIKOS

Research article

The role of evolutionary processes in determining trophic structure

Euan N. Furness^{1,2}, James D. M. Speed³, Russell J. Garwood^{4,5} and Mark D. Sutton⁶

¹Department of Zoology, University of Cambridge, Cambridge, UK

²Sidney Sussex College, University of Cambridge, Cambridge, UK

³Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

⁴Department of Earth and Environmental Sciences, University of Manchester, Manchester, UK

⁵Natural History Museum, London, UK

⁶Department of Earth Sciences and Engineering, Imperial College London, London, UK

Correspondence: Euan N. Furness (enf21@cam.ac.uk)

Oikos

2024: e10597

doi: [10.1111/oik.10597](https://doi.org/10.1111/oik.10597)

Subject Editor:

Emanuel A. Fronhofer

Editor-in-Chief: Dries Bonte

Accepted 9 September 2024



There are two contrasting hypotheses regarding the drivers of biomass-distribution among trophic levels within ecosystems. Energetic or bottom-up models propose control by supply of energy, either from autotrophy or from the underlying trophic level. Dynamical or top-down models propose control by predators in the overlying trophic level. Although multiple approaches have been used to reconcile these hypotheses, they have rarely considered the evolutionary pressures created by different distributions of biomass. Here, we study the effects of these evolutionary processes using an agent-based, spatially-explicit, eco-evolutionary model. We demonstrate that, when ecosystems are simple and predator-prey relationships between species are fixed and do not evolve, primary productivity limits the number of trophic levels. In this case, the abundance in the top trophic level is always limited by productivity. However, productivity-limited trophic levels subject those below them to limitation by predation, and predation-limited trophic levels allow trophic levels below them to grow until limited by productivity. These results match the expectations of the exploitation ecosystems hypothesis (EEH), which predicts the same pattern of alternating top-down and bottom-up control on trophic levels. When species are able to evolve to adaptively adjust their trophic levels, however, selection is liable to lead to collapse of the trophic pyramid through prey switching. Under these conditions, all trophic levels experience bottom-up control. When the evolution of prey switching is restricted, higher trophic levels are evolutionarily stable and the predictions of the EEH are once again met; the stability of long food chains is thus dependent on the difficulty associated with prey switching. These results suggest that, at least under the combinations of model parameters explored in this study, evolutionary limitation is key to maintaining trophic structure.

Keywords: agent-based simulation, evolutionary simulation, exploitation ecosystems hypothesis, foodchain length, intraguild predation, trophic levels



www.oikosjournal.org

© 2024 The Author(s). Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

The concept of the trophic level is widely used in ecology as a tool to understand the interactions between organisms within ecosystems (McNaughton et al. 1989, Jonsson 2017, Barbier and Loreau 2019, Cropp and Norbury 2020). However, the processes controlling the distribution of biomass among trophic levels are not always clear (Reuman et al. 2009, Eriksson et al. 2012, Hatton et al. 2015, Woodson et al. 2018, Barbier and Loreau 2019). There are two different classes of model that describe how biomass varies from trophic level to trophic level within ecosystems: energetic and dynamical (Barbier and Loreau 2019). Energetic models stress the importance of bottom-up control of ecosystems (Brown and Gillooly 2003, Hatton et al. 2015), where abundance at higher trophic levels is limited by the abundance of their prey. These models are characterised by predictions of pyramidal biomass distributions, which are generally resistant to stochastic perturbations (Barbier and Loreau 2019). In contrast, dynamical models stress top-down control of ecosystems (Volterra 1928, McCann et al. 1998), where the abundance of lower trophic levels is limited by their antagonistic interactions with their predators (Volterra 1928). Such models typically predict trophic cascades, where any change in the biomass of one trophic level results in the opposite change in the biomass of the level below (Borer et al. 2005, Ripple et al. 2016). In some cases, dynamical models may also predict oscillations in the biomasses of trophic levels (Volterra 1928). Leibold et al. (1997) and Barbier and Loreau (2019) argued that hypotheses based entirely on either one of these two paradigms are limited in their ability to make general claims about the behaviour of trophic levels, because ecosystems differ in which of the two paradigms best describe their behaviour, and over what timescales. Metabolic processes, related to body size, are commonly considered important (Brown et al. 2004). Understanding the factors that control organism abundances within ecosystems is key to understanding how the biodiversity and services found in those ecosystems might be conserved in the face of anthropogenic disturbances (Harfoot et al. 2014). As such, a variety of models have arisen that make predictions about when and why top-down or bottom-up control dominates within ecosystems (Barbier and Loreau 2019), such as the exploitation ecosystems hypothesis (EEH) (Oksanen et al. 1981).

The EEH (Oksanen et al. 1981) proposes that the abundances of organisms at different trophic levels within an ecosystem are regulated in a predictable way by a combination of top-down and bottom-up control, that varies along a gradient of productivity (Oksanen and Oksanen 2000, Oksanen et al. 2020). Specifically, it claims that the number of trophic levels within ecosystems increases with productivity, and that those trophic levels alternate down the food chain between being limited in biomass through predation pressure (top-down control) and by the productivity of the ecosystem as a whole (bottom-up control), with the highest trophic level always limited by productivity (Fretwell 1977, Oksanen et al. 1981). Like the synthetic model of Barbier and Loreau (2019), the EEH can be thought of as combining energetic

and dynamical processes in making predictions about the biomasses of distinct trophic levels. The EEH hence predicts a positive correlation between biomass and productivity only for those trophic levels that are productivity-limited. In the alternating levels limited instead by predation pressure, any biomass-gain from an increase in productivity is transferred to the level above (Fig. 1). The EEH has empirical support from a wide range of ecosystems (Eriksson et al. 2012, Ripple and Beschta 2012, Hoset et al. 2014), but does not apply to all (Post et al. 2000, Hatton et al. 2015).

Partly because it is unclear what processes control the distribution of biomass among trophic levels within ecosystems, it is also unclear what processes have the strongest, or most common, impact on the total number of trophic levels within ecosystems (Persson et al. 1992, Post 2002, Evans et al. 2005, Takimoto and Post 2012). Despite significant research into the importance of primary productivity in this context (Kaunzinger and Morin 1998, Arim et al. 2007, Ziegler et al. 2015, Oksanen et al. 2020), results have been mixed, with productivity apparently limiting the number of trophic levels in some cases (Kaunzinger and Morin 1998, Ziegler et al. 2015) but not others (Briand and Cohen 1987, Ayal and Groner 2009, Ward and McCann 2017). It is likely that different factors control the number of trophic levels in different ecosystems (Post 2002); these may include disturbance (Schneider 1997, Chanut et al. 2019), ecosystem size (Briand and Cohen 1987, Post et al. 2000), ecosystem age (Post 2002), the size-structure of food webs (Cohen et al. 1993, Ayal and Groner 2009, Sommer et al. 2018), or the ecological (Pimm and Lawton 1977) or evolutionary (Hastings and Conrad 1979) instability inherent in specialising on high-trophic-level food sources. The EEH predicts that, at least under some circumstances, the number of trophic levels within an ecosystem should be limited by the productivity of the ecosystem, although this prediction may be confined to seasonally cold, terrestrial environments where productivity is generally low (Oksanen et al. 2020).

Less attention has been paid to the influence of evolutionary processes on the number and size of trophic levels within ecosystems. Certain ecologically stable configurations of trophic levels may nevertheless be evolutionarily unstable if selection pressure favours prey switching: the process where organisms adapt their diets to maximise their energy supply (Oaten and Murdock 1975, Kondoh and Ninomiya 2009). Notably, predators may sometimes be selected to feed at a lower trophic level due to the substantial loss of energy associated with movement of biomass along food chains (Hastings and Conrad 1979). In some cases, this phenomenon has been suggested to limit the number of trophic levels in ecosystems (Kondoh and Ninomiya 2009), although there is debate over the circumstances in which this limit should apply (Brown and Gillooly 2003, Brown et al. 2004). Alternatively, predators may be selected to increase the trophic level at which they are feeding, at least in part, if efficient transfer of energy from one trophic level to the next is concentrating it at the top of the trophic pyramid (Brown et al. 2004). This process, where predators adapt to feed on other members of their own trophic level, is referred to as 'interference' by Oksanen et al. (1981) and also falls

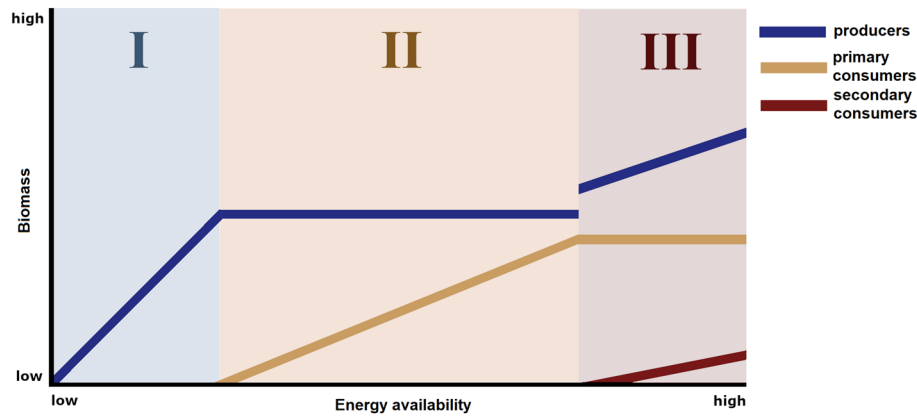


Figure 1. The predictions of the exploitation ecosystems hypothesis (EEH). At very low levels of productivity (zone I), primary consumers cannot exist at a stable population within the ecosystem and, as such, only producers are present. In the absence of primary consumers, the biomass of producers is dictated only by the availability of energy (bottom–up control) and therefore shows a correlation with productivity. Once producer biomass becomes sufficient to sustain a population of primary consumers (zone II), these consumers exert top–down control on the producers. Producer biomass in zone II is therefore independent of productivity, whereas the absence of secondary consumers means that primary consumer biomass is not subject to top–down control and is therefore limited only by the rate at which they can derive energy from the producers (i.e. productivity) (bottom–up control). Primary consumer biomass in zone II therefore scales with productivity. Once primary consumer biomass reaches a certain threshold, it is sufficient to support a stable population of secondary consumers (zone III). These secondary consumers exert top–down control on the primary consumers and, in so doing, limit the ability of the primary consumers to exert top–down control on the producers. As such, the biomass of primary consumers ceases to scale with productivity, whereas the biomass of producers resumes scaling with productivity. In the absence of any top–down control, the secondary consumers also experience bottom–up control and, as such, will also scale in biomass with productivity. Figure based on [Oksanen and Oksanen \(2000\)](#).

under the definition of intraguild predation ([Holt and Polis 1997](#)), which we use henceforth.

One limiting assumption made by the EEH ([Oksanen et al. 1981](#)) is that organisms occupy discrete trophic levels, obtaining all of their energy from the trophic level below (or through primary productivity, in the case of the lowest trophic level). However, the effect of violating this assumption, in ecosystems that would otherwise produce patterns as predicted by the EEH, is not clear. Here, we test how top–down and bottom–up control influence the distribution of biomass among trophic levels and the number of trophic levels found within ecosystems using the Rapid Evolutionary Simulator (REvoSim): an eco-evolutionary simulation model, which models the behaviour of individual organisms within a population over geological time ([Garwood et al. 2019](#), [Furness et al. 2023](#)). This model does not incorporate metabolic or body size differences among organisms, which have previously been highlighted as important drivers ([Brown et al. 2004](#)). We are thus able to test the extent to which biomass distributions can be explained in the absence of these factors, and to provide insight into the mechanisms by which they may drive distributions. We also test the stability of these influences in the face of evolutionary pressures, and compare these results to the predictions of the EEH.

Material and methods

The REvoSim system

We performed eco-evolutionary simulations in the Rapid Evolutionary Simulator (REvoSim ver. 3.0.1) ([Garwood et al.](#)

[2019](#), [Furness et al. 2023](#)). This program runs spatially explicit simulations of ecosystems, over evolutionary time, at the level of the individual organism. REvoSim is written in the C++ programming language, supplemented by the Qt framework (<https://www.qt.io>), and is freely available from GitHub (<https://github.com/palaeoware/revosim>), with a stable release archived at Zenodo (<https://zenodo.org/record/8228938>). Documentation is available at <https://revosim.readthedocs.io/en/v3.0.1>. A full description of REvoSim can be found in [Garwood et al. \(2019\)](#) and [Furness et al. \(2023\)](#), but a summary is provided here for convenience.

Each organism in REvoSim exists within one of 10 000 ‘cells’ in a 100 × 100 grid, and does not move during its lifetime. Each cell consists of 100 spatially undifferentiated ‘slots’, each of which can either contain one individual organism, or be vacant ([Fig. 2a](#)). Each cell has three independent abiotic variables, analogous to environmental conditions such as temperature, rainfall or soil type, which are visualised as the red, green and blue colour channels of an RGB image. These variables can be used to define spatial habitat heterogeneity, or varied over time to simulate temporal changes. Each organism in REvoSim possesses a binary genome composed of a number of 32 bit ‘words’ (independent sections of genome, analogous to chromosomes), each of which can be independently assigned to play a role in any number of processes that interact with organism genome content. In our experiments, genomes comprised either two or four 32-bit words, all of which influenced both the rate at which organisms could harvest energy from their abiotic environment, and inter-organism interaction outcomes. As a result, organisms experienced competing evolutionary pressures on their genomes, as mutations that improved environmental fitness

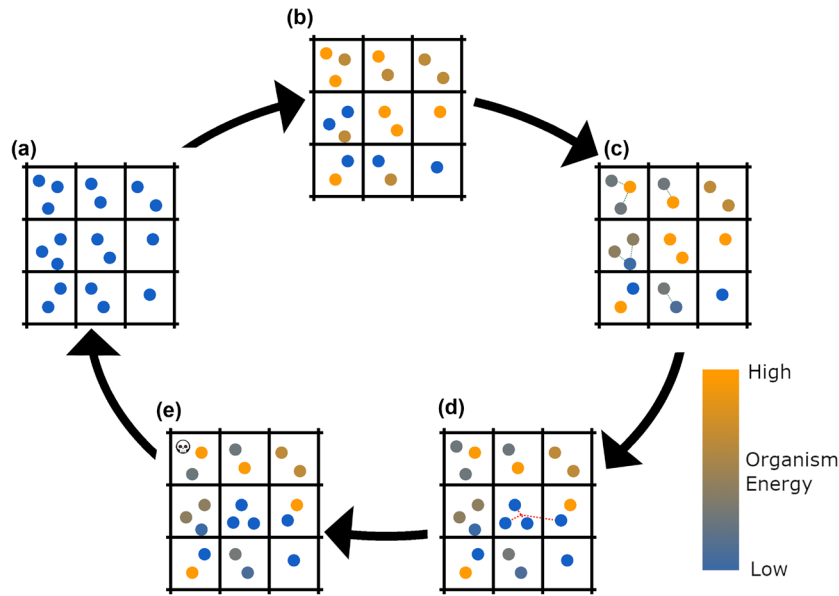


Figure 2. A diagram showing the basics of an iteration within the REvoSim model in a grid of nine cells. (a) Organisms exist within individual cells, and have individual genotypes; (b) organisms harvest energy from their abiotic environment; (c) organisms interact with other organisms in the same cell (green dotted lines), harvesting some fraction of their energy; (d) organisms with sufficient energy will expend that energy to reproduce (red dotted lines), passing on their genomes with the possibility of mutations; (e) organisms that have reached maximum age will die. This loop then repeats, with energy carried over between iterations. Here, organisms in (a) have zero energy, but this will only be the case at the start of the simulation.

were liable to reduce organisms' abilities to gain energy from interactions.

In REvoSim, each organism is assigned an 'environmental fitness', which describes how well adapted that organism is to collecting energy from its abiotic environment. In order to calculate this parameter, each word of an organism's genome is compared (using a boolean exclusive OR operation) with each of three environmental 'masks'. Each mask is a 32-bit binary number, the value of which is determined by either the red, blue or green colour channel of the organism's cell. The total number of 1s in the resulting binary sequences is summed, with environmental fitness determined by how close this sum is to a pre-set target value. This method ensures that 1) there are multiple ways to achieve maximal environmental fitness in any given environment and 2) there are many more ways to have low/zero environmental fitness than high environmental fitness (Garwood et al. 2019).

The ability of organisms to gain energy from inter-organism interactions is controlled by a similar mechanism. During an interaction, each word in the genome of the 'focal' organism (i.e. the one initiating the interaction) is compared (using a boolean exclusive OR operation) twice with each word in the genome of the other organism (the 'target' organism), once after being rotationally shifted one bit to the left, and once after being rotationally shifted one bit to the right. The number of 1s in the latter comparison is subtracted from the number of 1s in the former to create an 'interaction score'. The proportion of the target organism's energy that is lost during an interaction is determined by how close the interaction score is to a preset target value. This method guarantees

that 1) organisms with identical genomes will produce interaction scores of zero, and 2) reversal of the roles of two organisms in an interaction will change the sign of the interaction score (such that no organism may predate its own predator) (Furness et al. 2023). The full details of the predation mechanism are described in Furness et al. (2023).

Simulations run for a number of 'iterations'. In each iteration, each cell is provisioned with a fixed amount of energy, which is then divided among all occupants of that cell in proportion to their environmental fitness (Fig. 2b). The shape of the fitness landscape in REvoSim is determined in part by a variable called the 'settle tolerance'. The higher the settle tolerance, the greater the variety of genomes that are able to gather some energy from any given environment and the less difference each change to a genome makes to the rate at which an organism can gather energy from its environment (i.e. the less jagged the fitness landscape). Each organism in the simulation then attempts to harvest energy from those around it through interactions, with the success or failure of these interactions determined by the genomes of the two organisms involved (Fig. 2c). During successful interactions, some (configurable) fraction of energy is lost to reflect the inefficiency of energy transfer between trophic levels (Lindeman 1942, Andersen et al. 2009). This mechanism encourages the evolution of specialist predators that cannot themselves be predated by their prey, and the genomes of which differ substantially from the genomes of their prey. The trophic level (TL) of each organism is tracked over the course of its life, and is equal to one plus the mean of the trophic levels of all of the sources from which that organism has gained energy,

weighted by the proportion of its energy that has been gained from each of those sources. The abiotic environment is treated as having a trophic level of -1 for the purposes of this calculation. Thus, an organism A that obtained all of its energy from the abiotic environment would have a trophic level of zero. A second organism B that obtained all of its energy from organism A would have a trophic level of one. And a third organism C that obtained half of its energy from organism A and half from organism B would have a trophic level of 1.5.

Energy accumulates in organisms over multiple iterations. After a given organism (referred to here as the focal organism) has accumulated more than a threshold amount of energy, it will attempt to breed by selecting a partner organism from the same cell (Fig. 2d). The method of breeding is configurable, and may be either asexual, facultatively sexual or obligately sexual. Breeding in these experiments was facultatively sexual, and so each organism selected a random organism with enough stored energy (i.e. a breeding individual) from the same cell as the partner organism, and may have selected itself. Breeding will fail if the selected partner organism is too genetically dissimilar to the focal organism, with the threshold for genetic similarity set by the user. When breeding fails, organisms do not expend energy or reproduce in that iteration, and will reattempt breeding in the next iteration if they are still alive. Hybridisation between species is possible in REvoSim, but REvoSim's strict species definition makes it very rare (i.e. it can only occur if two populations become completely genetically isolated, and then later become genetically compatible by chance). Furthermore, breeding across trophic levels is expected to be very rare, since two genetically similar organisms inhabiting the same cell (and, therefore, the same environment), will tend to gather energy from the same sources. Offspring inherit genomes from their parents (half from each parent, on average, when breeding is sexual), with a possibility of a random mutation in one bit of the genome, and disperse from their parents' cell in a random direction and for a random distance. Offspring then settle within the cell into which they have dispersed and remain there for the rest of their lives. Dispersal distance is weighted towards low values and may be zero, in which case offspring settle in the same cell as their parents.

In all of our simulations, the values of environmental variables were kept constant both spatially and temporally (i.e. the environment was specified by a single homogenous and unchanging colour). The number of individuals in each trophic level was recorded every 50 iterations using the 'grid-TrophicHistograms' logging option, and each individual had a lifespan of 30 iterations (Fig. 2e). Harvesting of energy through interactions was non-lethal (equivalent to herbivores grazing on plant biomass), and so interactions did not reduce lifespans below 30 iterations. However, loss of energy will have reduced reproductive rate in the predated organisms, and will therefore have reduced their population size. In this respect, the REvoSim interactions system is in some ways more similar to a parasite–host system, and any phenomena that require direct killing of prey by predators will not be recovered by this system. Abundance was used as a

proxy for biomass in all simulations, as REvoSim organisms lack a defined body size, and organism traits that would be expected to co-vary with body size (e.g. lifespan) are constant among organisms in our simulations.

Experiment 1 – the role of primary productivity

In order to investigate the impact of primary productivity on the maximum number of trophic levels in REvoSim simulations, and their abundances, we initialised eight replicate simulations with five different organism genomes known to form a simple food chain of length five (cf. Furness et al. 2023 for an explanation of this feature); the apex predator of which immediately went extinct in all replicates due to the inefficiency of energy transfer through the chain. We selected the environment colour to ensure that only the genome at the start of the food chain could gather energy from the abiotic environment. Mutations were disabled and the genomes were too dissimilar to breed with each other; thus, no mechanism existed for genomic evolution, and the five genomes represented five fixed species, each at a different trophic level. Genome size in this experiment was two 32-bit words: smaller than in experiment 2 and 3, because in the absence of mutation or recombination the genome size is unimportant and a smaller genome allows for more efficient computation. Energy transfer efficiency was set to 50%. A value of 10–20% would be more representative of real-world ecosystems (Lindeman 1942, Andersoen et al. 2009), although this value is dependent upon body size (Brown et al. 2004). However, this increased efficiency was employed so that a viable population of organisms could be supported in higher trophic levels, given the limit to population size in REvoSim's cells. All of the settings for this experiment are recorded in the Supporting information.

These simulations were run for 145 000 iterations, during which the energy input to the simulation was experimentally varied so that the impact on the population sizes of different trophic levels could be observed. The energy input was varied over time in these simulations, rather than in space (i.e. between cells), because REvoSim's logging systems are better equipped to detect differences between logging iterations than between cells within a single iteration. Energy input was decreased gradually over time except following species extinctions, when it was reset to a high level to allow the new (less diverse) community to experience a wide range of energy levels. Energy was decreased over time, rather than increased, so that new trophic levels did not need to be added into the simulation continuously. Abundances of trophic levels were tracked by outputting the abundances of each genome (i.e. each species). The simulation was stopped after 145 000 iterations because the energy level had declined to a point where only one species (and therefore trophic level) was still alive.

Experiment 2 – evolutionary stability

To determine the evolutionarily stable state of the trophic levels within our simulations, we used REvoSim's reseed feature

to seed each of sixteen replicate simulations with three different organism genomes (= species), known to form a simple food chain of length three. Sixteen replicates were judged sufficient to ensure that any categorically different scenarios, resulting from REvoSim's randomised setup processes, would be detected (as occurred in experiment 3). The environment colour was selected to ensure that only one of the three was able to gather energy from the abiotic environment (see Furness et al. 2023 for an explanation of this feature). Mutations were disabled in these simulations for a 'burn-in' period of 10 000 iterations so that a stable ecosystem could be established, after which mutations were enabled for the remainder of the simulation. Settings for these simulations are recorded in the Supporting information.

Energy transfer efficiency was set to 30% so that a viable population of organisms could be supported in the third trophic level. A lower efficiency was used in this experiment than in experiment 1 because fewer trophic levels needed to be supported. Similarly, the settle tolerance was initially set to a high value (typically around 60, although this depended upon the random fitness landscape generated at the start of the simulation) to ensure that the producer genome was able to gather energy from the abiotic environment, but this value was reduced (over approximately 1000 iterations) to a value of 10 after mutations were enabled in order to reduce the probability that a well-adapted predator would arise that could also efficiently gather energy from the abiotic environment. Modifying the settle tolerance parameter in this way was necessary to ensure that populations of organisms could become established in the simulation during the burn-in period. Simulations were then run without setting changes for sufficient time to allow for an evolutionary equilibrium to be reached (200 000 iterations). Subsequently, energy was decreased gradually so that the impact on the population sizes of different trophic levels could be observed. Because the trophic level of an organism depended upon the interactions between its genome and the genomes of organisms around it, and novel genomes could arise through mutation and recombination, it was not possible to calculate the a priori trophic level of species from its genome alone. Instead, the abundance of each trophic level was tracked directly by recording, at every logging iteration, the trophic level of every living individual in the simulation (binned into bins of width 0.1). Fractional-width bins were used to account for the presence of organisms with non-integer trophic levels (i.e. those obtaining energy from multiple different sources, with different trophic levels). Organisms within these bins are likely to have represented a large number of different species, each interacting with locally adapted prey and predators within REvoSim's spatially explicit landscape.

Experiment 3 – intra-trophic level predation effects

To isolate the effect of intra-trophic level predation within our simulations, we repeated experiment 2, but with the 'restrict interactions' setting enabled so that, after the first 100 iterations, it was only possible for a predation event to occur if

the potential predator had a current trophic level at least 0.5 higher than the potential prey (Furness et al. 2023). The first 100 iterations were treated differently because all organisms were initialised with a trophic level of zero and, as such, a brief window of unrestricted interactions had to be allowed so that organisms' trophic levels could become established. This restriction made it much harder for organisms to either increase or decrease their trophic level (i.e. to engage in prey switching, including intraguild predation). All other settings and procedures were as in experiment 2 (Supporting information).

A comprehensive sensitivity analysis of the model parameters used in this experiment is outside of the scope of this study. Nevertheless, REvoSim uses many parameters (Supporting information), which are often assigned arbitrarily unless they are the study parameter, and the values assigned to some of these parameters could influence the results of our experiments. The majority of REvoSim's parameters are either not used in our study (e.g. 'environmental refresh rate'), or govern aspects of the simulation that are unlikely to influence the results given our experimental setup (e.g. 'dispersal' and 'chance of mutation', which are relatively unimportant on a homogenous and unchanging landscape). However, the organism lifespan and energy transfer efficiency parameters would be expected to influence our results: higher lifespans or transfer efficiencies would both be expected to result in more efficient transfer of energy to the top of food chains, and therefore more top-heavy distributions of organism abundance. The organism abundance distributions produced by alternative values of these two parameters are provided in the Supporting information. All other parameter values used to create these supplementary results are the same as in experiment 3.

Results

Experiment 1 – the role of primary productivity:

In experiment 1, a decrease in energy input resulted in a marked decrease in the abundance of the top trophic level (TL), and every second trophic level beneath that, but smaller and more complex changes in the abundance of the other trophic levels (Fig. 3, Supporting information). Decreases in energy input eventually resulted in the extinction of the top trophic levels.

Experiment 2 – evolutionary stability

In experiment 2, the secondary consumers ($TL \geq 2$) fell to negligible abundance during the equilibration phase, prior to the start of the systematic decrease in energy input (Supporting information). Although some organisms were still found to have $TL \geq 2$ over the course of the simulation, they were too rare to represent a self-sustaining species and must instead represent organisms capable of obtaining energy from both producers and primary consumers, which happen to not yet have interacted with any producers. Abundances of the two remaining trophic levels (producers and primary consumers) both showed clear positive relationships with

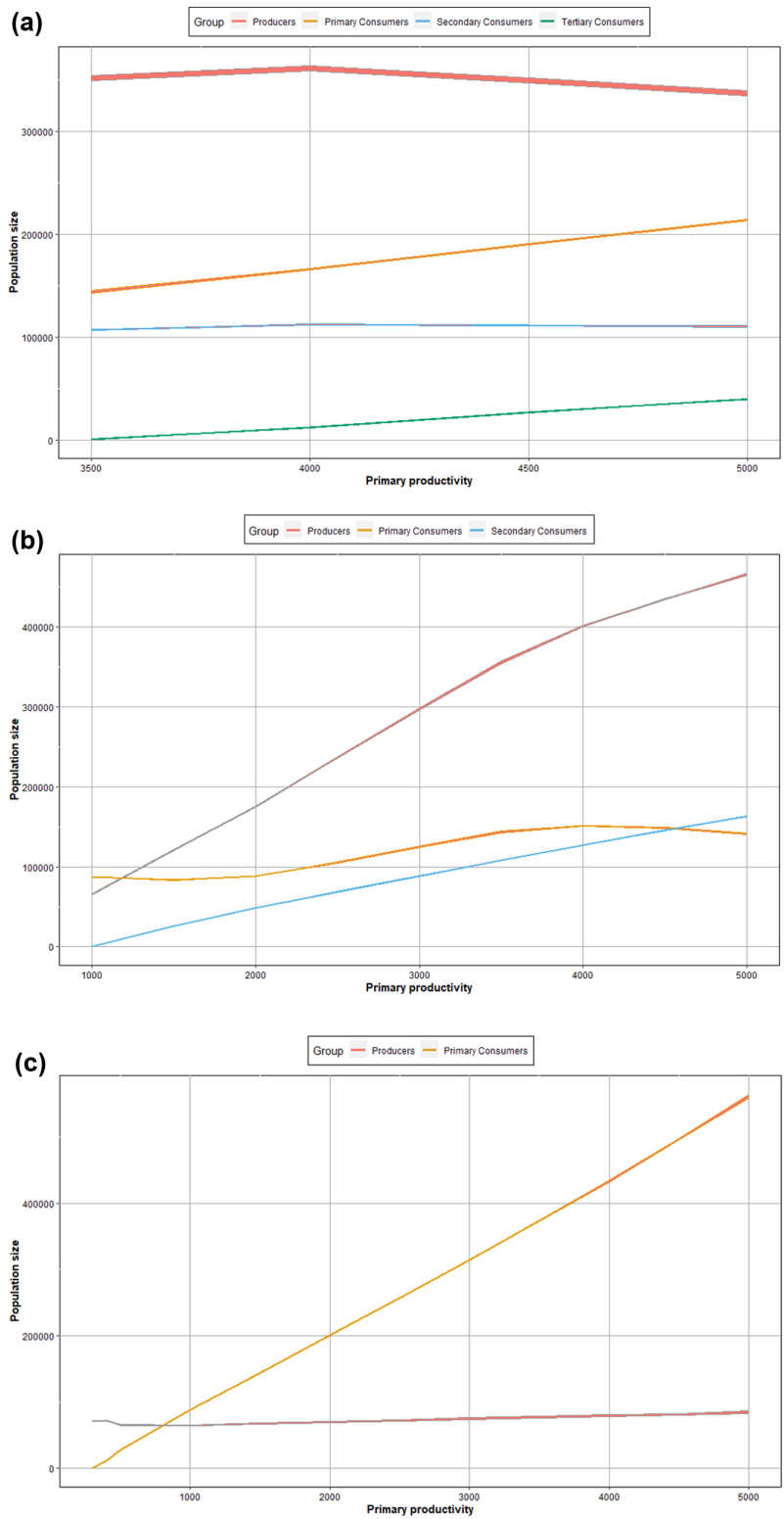


Figure 3. Relationships between productivity and the abundances of the four different genomes in experiment 1 ($n = 8$), (a) prior to any extinctions, (b) after the extinction of tertiary consumers, (c) after the extinction of secondary consumers. Lines connect points representing the mean population size recorded in all logging iterations and across all replicates for a given primary productivity value. Line thickness forms an envelope representing two standard deviations of the average values among replicates ($n = 8$). This variation is very small relative to the difference in abundance among trophic levels.

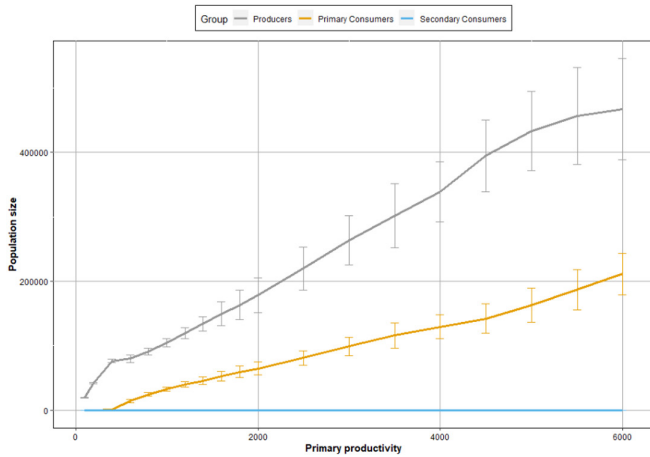


Figure 4. Changes over time in the abundances of organisms with different trophic levels in experiment 2. Lines connect points representing the mean population size recorded in all logging iterations and across all replicates for a given primary productivity value. Error bars represent one standard deviation of the average values among replicates ($n = 16$).

productivity (Fig. 4). Throughout this experiment, a non-negligible number of organisms (~5%) had trophic levels that exceeded integer values by more than 0.1 points, indicating multiple food sources with different trophic levels (Fig. 5, Supporting information). The proportion of these organisms showed a positive relationship with energy level when only a single trophic level was present (Fig. 5; blue region).

Experiment 3 – intra-trophic level predation effects

In experiment 3, where interactions occurred only between organisms with a difference in trophic level of at least 0.5, the abundance of secondary consumers remained non-negligible during the equilibration phase, unlike in experiment 2 (Supporting information). In this experiment, prior to the extinction of the secondary consumers, the abundance of the producers and secondary consumers showed a positive relationship with primary productivity, whereas the abundance of the primary consumers did not. However, subsequent to the extinction of the secondary consumers, the abundance of the primary consumers showed a positive relationship with energy level, whereas the abundance of the producers did not. After the extinction of the primary consumers, the abundance of the producers showed a positive relationship with energy level (Fig. 6). Throughout this experiment, very few organisms ($< 0.2\%$) had trophic levels that exceeded integer values by more than 0.1, suggesting that most organisms were not obtaining energy from multiple different trophic levels (Fig. 7). Those organisms that were obtaining energy from multiple sources almost exclusively had trophic levels around 1.9: secondary consumers, engaged in facultative consumption of producers (Supporting information).

Notably, in experiment 3, the relationship between the abundance of primary consumers ($1 \leq TL < 2$) and energy varied between replicates: in the majority of replicates, there was no relationship prior to the extinction of the secondary

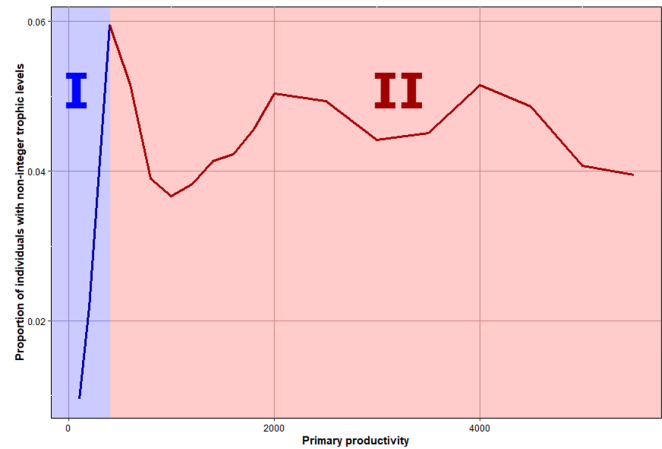


Figure 5. The mean proportion of individual organisms in the simulation in experiment 2 with a trophic level more than 0.1 point higher than an integer value ($n = 16$). The red region indicates the period of the simulations with two stable trophic levels. The blue region indicates the period of the simulations with one stable trophic level. Roman numerals correspond to the equivalent regions in Fig. 1. Lines connect points representing the mean proportion of individuals with non-integer trophic levels recorded in all logging iterations and across all replicates for a given primary productivity value.

consumers ($TL \geq 2$). However, in some replicates, a negative relationship could be observed at all energy levels (see the Supporting information for the relationships in each replicate).

Discussion

The objective of this study was to determine the role of evolutionary processes in controlling how productivity and predation pressure (bottom-up and top-down control respectively) dictate the number of trophic levels, and the abundances of organisms (equivalent to biomass, in REvoSim) within those trophic levels across gradients of productivity. Broadly, our results support the predictions of the exploitation ecosystems hypothesis when its assumption of integer trophic levels is met (Oksanen et al. 1981). However, our results also suggest that evolutionary processes favour violations of this assumption, introducing non-integer trophic levels, which reduce the abundance of high-trophic level individuals.

Experiment 1 modelled integer trophic levels in the absence of evolution, and recovered patterns broadly compatible with EEH predictions. The EEH predicts that the biomass of the highest trophic level, and every second trophic level below that ('bottom-up-controlled trophic levels'), should be limited by productivity. A consistent, positive relationship between energy level and abundance of organisms was indeed recovered only in these trophic levels (Fig. 3). Relationships between productivity and abundances in other trophic levels (those predicted to be limited in biomass by predation pressure rather than productivity - 'top-down-controlled trophic levels') were more complex. In some periods of experiment 1, there was a weak but positive relationship between productivity and the abundance of producers (i.e. producer abundance decreases as productivity decreases)

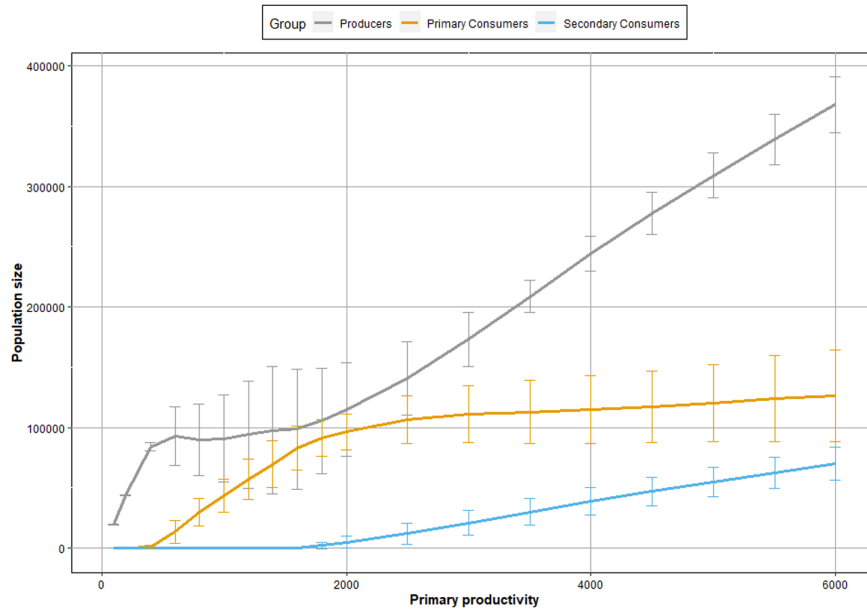


Figure 6. Changes over time in the mean abundances of organisms with different trophic levels in experiment 3. Lines connect points representing the mean population size recorded in all logging iterations and across all replicates for a given primary productivity value. Error bars represent one standard deviation of the average values among replicates ($n = 16$).

when the EEH would predict that there should be no such relationship (e.g. primary consumers between productivity values of 2000 and 4000 in Fig. 3b). This relationship can be attributed to a failure by primary consumers to totally suppress the growth of the producer population, although the reason for this occurring in these simulations is unclear.

The variation among replicates in the relationship between energy and the abundance of primary consumers in

experiment 3 (Supporting information) can be attributed to the genetic structure of organisms in REvoSim (Garwood et al. 2019, Furness et al. 2023): the effective fitness landscape in REvoSim is randomly generated in each replicate and, as such, in some replicates, it may be possible for primary consumers to evolve genotypes that could not be efficiently preyed by any other possible genotype. In such scenarios, the predation pressure, and therefore top-down population control, exerted on primary consumers by secondary consumers would be reduced, resulting in an increased relative role of bottom-up control of the population of primary consumers (i.e. a positive relationship between energy level and primary consumer population size). This hypothesis is supported by two observations that can be made in simulations where the abundance of primary consumers was a function of energy level prior to the extinction of secondary consumers: firstly, the abundance of primary consumers was larger than in other simulations and, secondly, the abundance of secondary consumers was smaller (Supporting information, replicate 1 and 3).

Overall, our results from experiment 2 and 3 demonstrate that EEH-type abundance distributions, where trophic levels alternate between being top-down and bottom-up controlled, can be stabilised over evolutionary time by placing limits on the ability of organisms to adapt to exploit available energy sources. In experiment 2, where such limits are absent, high energy inputs lead to an accumulation of primary consumers (Fig. 4), which produces an evolutionary incentive for primary consumers to become intraguild predators. Real-world ecosystems support this idea: if productivity controls the presence of top predators, then carnivore-carnivore predation will be more common in more productive ecosystems where top predators can feed on mesopredators (Elmhagen et al. 2010) and omnivores (Thompson et al.

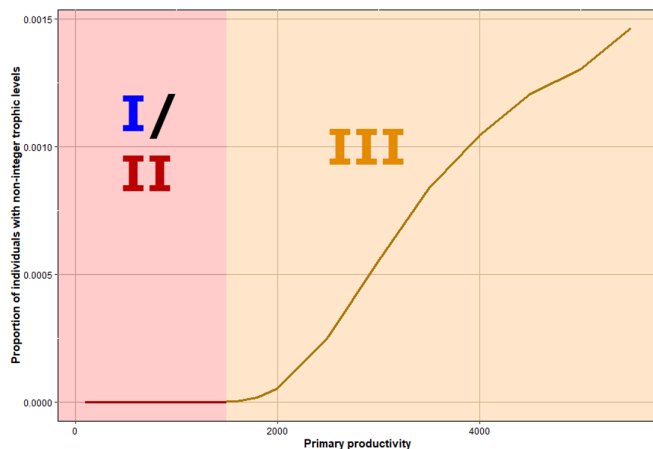


Figure 7. The mean proportion of individual organisms in the simulations in experiment 3 with a trophic level more than 0.1 point higher than an integer value ($n = 16$). The yellow region indicates the period of the simulations with three stable trophic levels. The red region indicates the period of the simulations with fewer than three stable trophic levels. Roman numerals correspond to the equivalent regions in Fig. 1. Lines connect points representing the mean proportion of individuals with non-integer trophic levels recorded in all logging iterations and across all replicates for a given primary productivity value.

2007). This increase in intraguild predation contributes to the abundance of non-integer trophic levels recorded in Fig. 5 (Hastings and Conrad 1979). It also reduces the abundance of consumers due to 1) the inefficiency of energy transfer during interactions, and resulting loss in energy within the consumer population, and 2) loss in efficiency of predation of producers by consumers resulting from consumers adapting to feed on multiple food sources. Both of these effects will reduce the predation pressure being exerted on producers (predation pressure that would otherwise prevent the abundance of producers from being linked to productivity). As a result, the producers will increase in abundance until a new evolutionarily stable state is reached (Fig. 4), while primary consumers will be less abundant than would be expected in the absence of intraguild predation. The relative abundance of producers will also create an evolutionary incentive for secondary consumers to engage in prey switching and become primary consumers. Such prey switching may contribute to the collapse of the secondary consumer tier early in experiment 2. This is congruent with Drossel et al. (2004), which demonstrated that the maintenance of complex, highly-tiered trophic levels in model systems was dependent upon predators focussing on specific prey species. In the absence of obligate consumers, any increase in productivity leads to an increase in the selection pressure on producers to act as facultative consumers, as demonstrated by the positive relationship between energy level and the proportion of organisms with non-integer trophic levels in the absence of obligate consumers (Fig. 5; blue region). Facultative herbivory by producers is less common in nature than facultative omnivory by herbivores, but hemiparasitic plants sourcing nutrients from host plants as well as photosynthesising themselves, provide real-world examples (Press and Phoenix 2005).

When intraguild predation and prey switching is restricted (experiment 3), the proportion of individuals with non-integer trophic levels is much lower (Fig. 7), and EEH-type abundance distributions are evolutionarily stable (Fig. 6). Sorting of organisms into trophic level bins of width 0.1 in experiment 2 and 3 prevented organisms with non-integer trophic levels from being detected as such if their trophic level exceeded an integer value by less than 0.1. However, this is very unlikely to have been an issue for the comparison of frequencies of non-integer trophic level organisms between experiment 2 and 3, as the detected frequencies differed by more than an order of magnitude. The shift from EEH-type abundance distributions to bottom-heavy pyramids in the presence of prey switching implies a proportionally greater role for bottom-up control (Barbier and Loreau 2019), and less potential for overexploitation of prey (Vuorinen et al. 2021). In such a bottom-up dominated ecosystem, trophic cascades should have less effect on biomass distributions (Barbier and Loreau 2019). Our finding that intraguild predation should dampen the effects of trophic cascades comports with existing theoretical work (Hart 2002) and empirical observations (Finke and Denno 2004, 2005, He et al. 2021).

In our simulations, secondary consumers were only evolutionarily stable when intraguild predation and prey

switching was limited (compare Fig. 4, 6). Intraguild predation is not frequently discussed as a driver of the number of trophic levels within ecosystems (although see Ward and McCann 2017). Furthermore, when it is, it is usually framed as driving a fractional increase in the number of trophic levels, since the effective trophic level of a predator engaging in intraguild predation will be higher than that of a predator that is not (Holt and Polis 1997). Instead, research into the drivers of food-chain length has tended to focus on productivity (Kaunzinger and Morin 1998, Arim et al. 2007, Ziegler et al. 2015, Oksanen et al. 2020), disturbance (Schneider 1997, Chanut et al. 2019) and ecosystem size (Briand and Cohen 1987, Post et al. 2000). Nevertheless, Oksanen et al. (1981) suggested that intraguild predation by secondary consumers could substitute for the presence of tertiary consumers at high energy levels. In our simulations, we observe the same phenomenon at a lower trophic level, since real-world limitations on the ability of herbivores to engage in intraguild predation (Hastings and Conrad 1979, Diehl 2003, Thompson et al. 2007) are not applicable in our model. In the presence of intraguild predation, tertiary consumers that could be supported by the productivity of the ecosystem may be absent because intraguild predation by secondary consumers limits the biomass of secondary consumers and allows the biomass of the primary consumer tier to increase. This pushes organisms that would be tertiary consumers to undergo prey switching, and to feed at a lower trophic level instead (Hastings and Conrad 1979).

The importance of prey switching within predator populations may contribute to the apparent role of body size ratios between trophic levels in controlling the number of these levels within ecosystems (Post 2002, Ayal and Groner 2009). The capacity for predators to change their food source may correlate with the body size ratio between adjacent trophic levels within an ecosystem, since prey switching to a higher trophic level (through intraguild predation) can only occur if organisms normally adapted for preying trophic level n also have the capacity to predate trophic level $n + 1$. Similarly, prey switching to lower trophic level can only occur if organisms normally adapted for preying trophic level n also have the capacity to incidentally predate trophic level $n - 1$. Both of these conditions are less likely to be met if organisms in trophic level $n + 1$ are much larger than organisms in trophic level n . This mechanism has previously been hinted at by considerations of the importance of factors such as predator gape size in empirical systems (Hairston and Hairston 1993, Gravel et al. 2013, Renneville et al. 2015). Furthermore, previous modelling studies have often incorporated body size related restrictions on predation behaviour into their simulation methods (although these studies have not generally resulted in the loss of non-integer trophic levels; Loeuille and Loreau 2005, Allhoff et al. 2015). Our study provides experimental support for the hypothesis that restrictions on predation contribute to the regulation of the number of trophic levels within ecosystems, as suggested by Drossel et al. (2004).

Conclusion

Our simulation analyses find broad support for the exploitation ecosystems hypothesis (EEH) when its assumption of integer trophic levels is met and when predation is efficient: abundance in the top trophic level, and every second trophic level below that, is positively correlated with productivity, whereas abundance in other trophic levels is not. However, the assumption of integer trophic levels was not evolutionarily stable within our system when no restrictions were placed on which other organisms individuals can interact with to obtain energy. Instead, populations were evolutionarily driven to engage in prey switching through both intraguild predation and feeding at lower trophic levels. Abundance distributions then transform from EEH-type to bottom-up dominated, bottom-heavy pyramids, where the abundances of all trophic levels have a positive relationship with productivity. This comports with existing theory on the impact of intraguild predation on trophic cascades. However, if prey switching is restricted a priori, then EEH-type abundance distributions persist in the presence of evolutionary processes. Further exploration of REvoSim's parameter space would be useful to determine the generality of this result.

The capacity for prey switching also results in evolutionary instability in higher trophic levels, resulting in an overall reduction in the number of trophic levels relative to equivalent systems without prey switching. This evolutionary instability provides a non-metabolic explanation for observed real-world relationships between predator:prey body size ratios, feeding modes and the number of trophic levels within ecosystems.

Acknowledgements – The authors thank three reviewers and the subject editor Dr. Emanuel A. Fronhofer for their comments on the manuscript.

Funding – ENF was supported by funding from the Natural Environment Research Council (NERC award NE/S007415/1). RJG was supported by NERC award NE/T000813/1.

Author contributions

Euan N. Furness: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (supporting); Writing – original draft (equal); Writing – review and editing (equal).

James D. M. Speed: Conceptualization (supporting); Writing – review and editing (equal). **Russell J. Garwood:** Software (lead); Writing – review and editing (equal). **Mark D. Sutton:** Funding acquisition (equal); Software (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Simulation code used in this study is freely available from GitHub (<https://github.com/palaeoware/revosim>), with a stable release archived at Zenodo (<https://zenodo.org/record/8228938>). Data used in this study are included in this submission as Supporting information.

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Allhoff, K. T., Ritterskamp, D., Rall, B. C., Drossel, B. and Guill, C. 2015. Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. – *Sci. Rep.* 5: 10955.
- Anderson, K. H., Beyer, J. E. and Lundberg, P. 2009. Trophic and individual efficiencies of size-structured communities. – *Proc. R. Soc. B* 276: 109–114.
- Arim, M., Marquet, P. A. and Jaksic, F. M. 2007. On the relationship between productivity and food chain length at different ecological levels. – *Am. Nat.* 169: 62–72.
- Ayal, Y. and Groner, E. 2009. Primary consumer body size and food-chain length in terrestrial communities. – *Isr. J. Ecol. Evol.* 55: 329–343.
- Barbier, M. and Loreau, M. 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. – *Ecol. Lett.* 22: 405–419.
- Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D. and Halpern, B. S. 2005. What determines the strength of a trophic cascade? – *Ecology* 86: 528–537.
- Briand, F. and Cohen, J. E. 1987. Environmental correlates of food chain length. – *Science* 238: 956–960.
- Brown, J. H. and Gillooly, J. F. 2003. Ecological food webs: high-quality data facilitate theoretical unification. – *Proc. Natl. Acad. Sci. USA* 100: 1467–1468.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. 2004. Toward a metabolic theory of ecology. – *Ecology* 85: 1771–1789.
- Chanut, P. C. M., Siebers, A. R. and Robinson, C. T. 2019. Flood disturbance affects macroinvertebrate food chain length in an alluvial river floodplain. – *Freshwater Biol.* 65: 490–501.
- Cohen, J. E., Pimm, S. L., Yodzis, P. and Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. – *J. Anim. Ecol.* 62: 67–78.
- Cropp, R. and Norbury, J. 2020. The emergence of new trophic levels in eco-evolutionary models with naturally-bounded traits. – *J. Theor. Biol.* 496: 110264.
- Diehl, S. 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. – *Ecology* 84: 2557–2567.
- Drossel, B., McKane, A. J. and Quince, C. 2004. The impact of nonlinear functional responses on the long-term evolution of food web structure. – *J. Theor. Biol.* 229: 539–548.
- Elmhagen, B., Ludwig, G., Rushton, S. P., Helle, P. and Lindén, H. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. – *J. Anim. Ecol.* 79: 785–794.
- Eriksson, B. K., Rubach, A., Batsleer, J. and Hillebrand, H. 2012. Cascading predator control interacts with productivity to determine the trophic level of biomass accumulation in a benthic food web. – *Ecol. Res.* 27: 203–210.
- Evans, K. L., Warren, P. H. and Gaston, K. J. 2005. Species–energy relationships at the macroecological scale: a review of the mechanisms. – *Biol. Rev. Camb. Phil. Soc.* 80: 1–25.
- Finke, D. L. and Denno, R. F. 2004. Predator diversity dampens trophic cascades. – *Nature* 429: 407–410.

- Finke, D. L. and Denno, R. F. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. – *Ecol. Lett.* 8: 1299–1306.
- Fretwell, S. D. 1977. The regulation of plant communities by the food chains exploiting them. – *Perspect. Biol. Med.* 20: 169–185.
- Furness, E. N., Garwood, R. J. and Sutton, M. D. 2023. REvoSim v3: a fast evolutionary simulation tool with ecological processes. – *J. Open Source Softw.* 8: 5284.
- Garwood, R. J., Spencer, A. R. T. and Sutton, M. D. 2019. REvoSim: organism-level simulation of macro and microevolution. – *Palaeontology* 62: 339–355.
- Gravel, D., Poisot, T., Albouy, C., Velez, L. and Mouillot, D. 2013. Inferring food web structure from predator–prey body size relationships. – *Methods Ecol. Evol.* 4: 1083–1090.
- Hairton, N. G. and Hairton, N. G. 1993. Cause–effect relationships in energy flow, trophic structure and interspecific interactions. – *Am. Nat.* 142: 379–411.
- Harfoot, M. B. J., Newbold, T., Tittensor, D. P., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M. J., Scharlemann, J. P. W. and Purves, D. W. 2014. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. – *PLoS Biol.* 12: e1001841.
- Hart, D. R. 2002. Intraguild predation, invertebrate predators, and trophic cascades in lake food webs. – *J. Theor. Biol.* 218: 111–128.
- Hastings, H. M. and Conrad, M. 1979. Length and evolutionary stability of food chains. – *Nature* 282: 838–839.
- Hatton, I. A., McCann, K. S., Fryxell, J. M., Davies, T. J., Smerlak, M., Sinclair, A. R. E. and Loreau, M. 2015. The predator–prey power law: biomass scaling across terrestrial and aquatic biomes. – *Science* 349: aac6284.
- He, H., Ning, X., Chen, K., Li, Q., Li, K., Liu, Z. and Jeppesen, E. 2021. Intraguild predation dampens trophic cascades in shallow aquatic mesocosms in the subtropics: implications for lake restoration by biomanipulation. – *Freshwater Biol.* 66: 1571–1580.
- Holt, R. D. and Polis, G. A. 1997. A theoretical framework for intraguild predation. – *Am. Nat.* 149: 745–764.
- Hoset, K. S., Kyrö, K., Oksanen, T., Oksanen, L. and Olofsson, J. 2014. Spatial variation in vegetation damage relative to primary productivity, small rodent abundance and predation. – *Ecography* 37: 894–901.
- Jonsson, T. 2017. Conditions for Eltonian pyramids in Lotka–Volterra food chains. – *Sci. Rep.* 7: 10912.
- Kaunzinger, C. M. K. and Morin, P. J. 1998. Productivity controls food-chain properties in microbial communities. – *Nature* 395: 495–497.
- Kondoh, M. and Ninomiya, K. 2009. Food-chain length and adaptive foraging. – *Proc. R. Soc. B* 276: 3113–3121.
- Leibold, M. A., Chase, J. A., Shurin, J. B. and Downing, A. L. 1997. Species turnover and the regulation of trophic structure. – *Annu. Rev. Ecol. Syst.* 28: 467–494.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. – *Ecology* 23: 399–417.
- Loeuille, N. and Loreau, M. 2005. Evolutionary emergence of size-structured food webs. – *Proc. Natl. Acad. Sci. USA* 102: 5761–5766.
- McCann, K. S., Hastings, A. and String, D. R. 1998. Trophic cascades and trophic trickles in pelagic food webs. – *Proc. R. Soc. B* 265: 205–209.
- McNaughton, S. J., Oesterheld, M., Frank, D. A. and Williams, K. J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. – *Nature* 341: 142–144.
- Oaten, A. and Murdoch, W. W. 1975. Switching, functional response and stability in predator–prey systems. – *Am. Nat.* 109: 299–318.
- Oksanen, L. and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. – *Am. Nat.* 155: 703–723.
- Oksanen, L., Fretwell, S. D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. – *Am. Nat.* 118: 240–261.
- Oksanen, T., Oksanen, L., Vuorinen, K. E. M., Wolf, C., Mäkynen, A., Olofsson, J., Ripple, W. J., Virtanen, R. and Utsi, T. Aa. 2020. The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the exploitation ecosystem hypothesis. – *Ecography* 43: 1859–1877.
- Persson, L., Diehl, S., Johansson, L., Andersson, G. and Hamrin, S. F. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. – *Am. Nat.* 140: 59–84.
- Pimm, S. L. and Lawton, J. H. 1977. Number of trophic levels in ecological communities. – *Nature* 268: 329–331.
- Post, D. M. 2002. The long and short of food-chain length. – *Trends Ecol. Evol.* 17: 269–277.
- Post, D. M., Pace, M. L. and Hairston, N. G. 2000. Ecosystem size determines food-chain length in lakes. – *Nature* 405: 1047–1049.
- Press, M. C. and Phoenix, G. K. 2005. Impacts of parasitic plants on natural communities. – *New Phytol.* 166: 737–751.
- Renneville, C., Le Rouzic, A. L., Baylac, M., Millot, A., Loisel, S. and Edeline, E. 2015. Morphological drivers of trophic cascades. – *Oikos* 125: 1193–1202.
- Reuman, D. C., Mulder, C., Banašek-Richter, C., Cattin Blandinier, M.-F., Breure, A. M., Den Hollander, H., Kneitel, J. M., Raffaelli, D., Woodward, G. and Cohen, J. E. 2009. Allometry of body size and abundance in 166 food webs. – In: Caswell, H. (ed.), *Advances in ecological research*, vol. 41. Elsevier Science Publishing Co. Inc., pp. 1–44.
- Ripple, W. J. and Beschta, R. L. 2012. Large predators limit herbivore densities in northern forest ecosystems. – *Eur. J. Wildl. Res.* 58: 733–742.
- Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., Motley, J. L., Self, K. E., Taylor, D. S. and Wolf, C. 2016. What is a trophic cascade? – *Trends Ecol. Evol.* 31: 842–849.
- Schneider, D. W. 1997. Predation and food web structure along a habitat duration gradient. – *Oecologia* 110: 567–575.
- Sommer, U., Charalampous, E., Scotti, M. and Moustaka-Gouni, M. 2018. Big fish eat small fish: implications for food chain length? – *Commun. Ecol.* 19: 107–115.
- Takimoto, G. and Post, D. M. 2012. Environmental determinants of food-chain length: a meta-analysis. – *Ecol. Res.* 28: 675–681.
- Thompson, R. M., Hemberg, M., Starzomski, B. M. and Shurin, J. B. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. – *Ecology* 88: 612–617.
- Volterra, V. 1928. Variations and fluctuations in the number of individuals in animal species living together. – *ICES J. Mar. Sci.* 3: 3–51.
- Vuorinen, K. E. M., Oksanen, T., Oksanen, L., Vuorisalo, T. and Speed, J. D. M. 2021. Why don't all species overexploit? – *Oikos* 130: 1835–1848.
- Ward, C. L. and McCann, K. S. 2017. A mechanistic theory for aquatic food chain length. – *Nat. Commun.* 8: 2028.
- Woodson, C. B., Schramski, J. R. and Joye, S. B. 2018. A unifying theory for top-heavy ecosystem structure in the ocean. – *Nat. Commun.* 9: 23.
- Ziegler, J. P., Solomon, C. T., Finney, B. P. and Gregory-Eaves, I. 2015. Macrophyte biomass predicts food chain length in shallow lakes. – *Ecosphere* 6: 1–16.