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RESEARCH

The biological cropping hypothesis over evolutionary time: an experimental test

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Abstract

Ecological disturbance has been proposed to have a variety of effects on biodiversity. These mechanisms are well studied over shorter timescales through experimental manipulation of ecosystems, but the effect of disturbance on longer timescales, where evolutionary processes operate, is less well understood. This is at least in part because evolutionary processes are too slow to observe in experimental manipulations of ecosystems. Here, we use the Rapid Evolutionary Simulator system (REvoSim) to solve this problem. REvoSim is a spatially explicit, agent-based simulation tool that models both ecological and evolutionary processes and is capable of simulating many thousands of generations of evolution per hour in a population of up to 1 million organisms. We use REvoSim to evaluate the biological cropping hypothesis, which predicts that the non-selective culling of organisms from populations ("cropping") can enhance diversity in those populations over long timescales by reducing the homogenising effects of competitive exclusion. Our experiments demonstrate that cropping alone *can* increase diversity within populations under certain circumstances: those where it has the net effect of reducing the selection pressure acting on those populations. However, intense cropping pressure may *increase* the selection pressure on organisms to reproduce rapidly, potentially offsetting the effects of reduced competitive exclusion on diversity. We also show that cropping alone is not sufficient to result in reproductive isolation within populations. This implies that, while cropping can maintain a high species diversity within an ecosystem, additional mechanisms must be invoked to generate that high diversity in the first instance.

Keywords Biological cropping · Agent-based simulation · Evolutionary ecology · Disturbance · Predator–prey dynamics

Introduction

Disturbance and biodiversity

A variety of mechanisms have been proposed through which disturbance might influence the biodiversity of ecosystems, either by removing species from ecosystems or by enabling species to survive when they otherwise could not. These mechanisms are here divided into non-neutral and neutral groups (Hubbell 2001). Non-neutral mechanisms model disturbance through its effects on the capacity of species to adapt to unique ecological niches. In this context, the patch-mosaic and intermediate disturbance hypotheses propose that disturbance increases biodiversity by increasing the availability of ecological niches (Grassle and Sanders 1973; Roxburgh et al. 2004). Additionally, disturbance has been proposed to increase biodiversity by reducing population sizes. In so doing, it is suggested that disturbance permits prey species to survive with narrower niches, containing only their favoured resources, thus reducing competitive exclusion rates (Huston 1979). However, disturbance has also been proposed to decrease diversity by eliminating occupied niches within ecosystems (Sandel et al. 2011; Cook et al. 2017), or by decreasing the ability of organisms to specialise to ecological niches where they exist (Fine 2015; Furness et al. 2021a).

By contrast, neutral disturbance mechanisms are not concerned with ecological niches, but instead act directly on the populations of organisms themselves, generally by removing

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individuals from populations. In this context, disturbance (in the form of predation or pathogens) has been proposed to increase biodiversity by selecting against common genotypes (Paine 1966; Gendron 1987; Comita et al. 2014). Additionally, the biological cropping hypothesis proposes that disturbance increases biodiversity by reducing the effect of competitive exclusion within niches (Dayton and Hessler 1972; Huston 1979). Alternatively, the more-individuals hypothesis proposes that disturbance decreases biodiversity by reducing the abundances of species within ecosystems, thereby increasing their risk of extinction (Storch et al. 2018).

While the timescales that these hypotheses are typically applied to vary, eco-evolutionary theory suggests that factors that affect biodiversity on one timescale should also influence it on others (Fussman et al. 2007). Disturbance that allows for the existence of a species within an ecosystem over ecological time (e.g. years to hundreds of years) can only do so if repeated disturbance over evolutionary time has created a steady supply of disturbed ecosystems within which disturbance-tolerant species are not outcompeted by disturbance-averse species. Consequently, disturbance that increases or decreases the biodiversity of ecosystems over a period of many millions of years must also have a proportional effect, on average at least, over much shorter time periods. Therefore, two hypotheses that propose opposite effects of disturbance on biodiversity in natural ecosystems are in conflict even if the timescales that they are framed in are very different. The same is not true for considerations of spatial scale, since species' presence and absence can vary in space across an ecosystem such that a disturbance may simultaneously reduce small-scale (alpha) diversity (Lambshead et al. 2001; Evanno et al. 2009) and increase large-scale (gamma) diversity (Grassle and Sanders 1973; Furness et al. 2021a).

Testing the predictions of these conflicting hypotheses has historically been difficult (McClain and Schlacher 2015; Paulus 2021). Experiments involving the manipulation of ecosystems are, for practical and ethical reasons, generally conducted on small scales (Paine 1966; Thistle et al. 2008; Hart and Jenkins 2023). Consequently, they cannot necessarily predict the response of biodiversity to disturbance on the spatial scale of entire ecosystems (Grant 2000). Observational studies can operate at larger spatial scales but, as variables cannot be manipulated, they cannot necessarily conclude that observed correlations are causatively linked, merely that they are consistent with one hypothesis or another (Rex 1976; Schratzberger et al. 2009; McClain and Barry 2010). Furthermore, the imposition of an artificial disturbance regime on an ecosystem necessarily removes it from eco-evolutionary equilibrium. Consequently, observed biodiversity changes may be influenced by communities not having had time to equilibrate to their new disturbance regime through, for example, specialisation to newly available niches.

Eco-evolutionary simulations provide the opportunity to directly observe the effects of disturbance on species richness. Unlike empirical observations, simulations of ecosystems can precisely control potential confounding factors (Barido-Sottani et al. 2020; Hagen 2023). Furthermore, manipulation of disturbance regimes in simulation studies can be conducted over any desired spatial scale and can allow for ecosystems to reach new eco-evolutionary equilibria through the origination of new species. The use of eco-evolutionary simulation tools to model the effects of disturbance on ecosystems is not new (Rangel et al. 2018; Furness et al. 2021a), but the biological cropping hypothesis (Dayton and Hessler 1972) has not yet been evaluated using a simulation approach.

The biological cropping hypothesis

The biological cropping hypothesis proposes that intense predation within ecosystems can increase biodiversity over evolutionary timescales (Dayton and Hessler 1972). Within many ecosystems, the abundance of organisms is limited by the availability of resources, for example, water, light, or nutrients in plants (Briones et al. 1998; Craine and Dybzinski 2013), or food in animals (Vahl et al. 2005). However, the biological cropping hypothesis is proposed to operate in ecosystems where resources are not the limiting factor; ecosystems where intense predation reduces the abundance of prey populations such that the ability of prey organisms to reproduce successfully is determined not by their ability to compete for resources, but rather by whether or not they avoid being predated. If the ability of an organism to avoid being predated does not respond strongly to selection, then organisms in such ecosystems would be expected to be under little selection pressure, and differences in competitive ability among prey species would not be expected to cause differential rates of population growth. Consequently, the competitive exclusion of weak competitors by strong competitors should not occur or should occur very slowly. In the absence of competitive exclusion, biodiversity may accumulate over time even if different species occupy near-identical Hutchinsonian niches (Dayton and Hessler 1972).

The biological cropping hypothesis shares some features with the hypothesis of diversification through negative frequency-dependent selection (Gendron 1987; Comita et al. 2014), and support for the latter is widespread (Pacala and Crawley 1992). However, at the most fundamental level, these hypotheses differ: the hypothesis of negative frequency-dependent selection proposes that a diversity of prey is maintained because predators and pathogens disproportionately target abundant organisms, thus selecting for rare phenotypes. By contrast, the biological cropping hypothesis proposes that predators predate prey indiscriminately (a process termed "cropping"). The biological cropping hypothesis does not require that predators be selective in their choice of prey, or even that they have any ability to recognise different prey phenotypes (Dayton and Hessler 1972; Huston 1979). Observational evidence suggests that non-selective predation is a common feature of certain ecosystems, such as the deep marine benthos, where biological cropping has been proposed as a driver of biodiversity (Briggs 1985; Gage 1996).

As biological cropping does not select for any particular prey phenotypes, it is an ecologically neutral process (Hubbell 2001). It does not create selection pressure against common phenotypes but rather preserves rare phenotypes when they might otherwise be selected against. The biological cropping hypothesis requires that competition for resources in the environment, which could result in divergent selection (Rundle and Nosil 2005), be suppressed by cropping. Consequently, in ecosystems where biological cropping is proposed to maintain high biodiversity, biodiversity cannot be driven by partitioning of resources through ecological speciation (Schluter 2001). This is entirely plausible: sporadic range disjunctions (White 1988; Johnson and Cicero 2004), genetic mechanisms (Rieseberg and Blackman 2010; Weiss-Schneeweiss et al. 2013), and sexual selection (Kondrashov and Shpak 1998; Panhuis et al. 2001) can all cause speciation in the absence of ecological selection. Furthermore, the suppression of competition for resources in the environment means that even poor competitors that immigrate into the community are liable to survive to increase standing biodiversity.

The biological cropping hypothesis was originally proposed as an explanation of the apparent diversity of the ecosystems of the deep seafloor (Dayton and Hessler 1972). However, it was not the only explanation proposed: other authors proposed that the diversity of the seafloor could be attributed to fine niche partitioning in an exceptionally stable environment (Sanders 1968), or fine niche partitioning as a result of intense predation (Glasser 1979), or specialisation to individual habitats within a spatiotemporal mosaic of habitat types created by disturbance (Grassle and Sanders 1973). At least partially due to the difficulties in studying deep-marine ecosystems, this debate remains unresolved (McClain and Schlacher 2015; Paulus 2021).

As with other real-world experiments studying the effects of disturbance on biodiversity (Paine 1966; Buckling et al. 2000; Hart and Jenkins 2023), tests of the biological cropping hypothesis tend to have been conducted at small spatial scales. One of the most popular methods has involved the use of predator-exclusion cages (Gallucci et al. 2008; Thistle et al. 2008), the hypothesis being that if the presence of predators increases biodiversity, then their exclusion should reduce it. However, these cages necessarily allow for migration of prey species into the sample from outside and, consequently, even if biological cropping is responsible for maintaining biodiversity in the ecosystem as a whole, migration of a biodiverse prey fauna into the cages from outside may limit the ability of cage experiments to detect an effect of predator exclusion (Grant 2000; Paulus 2021). Furthermore, any evolutionary effect of predator exclusion will not be detected by these experiments, since real-world evolutionary processes will be too slow to be noticeable over the timescale of cage experiments.

Here, we overcome these limitations using the eco-evolutionary simulation tool REvoSim (Garwood et al. 2019; Furness et al. 2023). The biological cropping hypothesis would predict that diversity will be higher in the presence of cropping (i.e. when population sizes are limited by cropping rather than by productivity), than in populations of a similar size where cropping is absent. We compare the diversities recorded in simulations with and without biological cropping, and in a third scenario where population sizes are limited by neither cropping nor productivity, but rather by the availability of physical space in the ecosystem. Limitation of population sizes by substrate space is common in nature, particularly in low-trophic sessile organisms (e.g. in kelp (Reed 1990), and lichen (Armstrong and Welch 2007)). This provides an alternative scenario where selection for efficiency of energy extraction will be suppressed, as energy is not limiting. Comparison of the results of the space-limited and cropping scenarios is intended to enable decoupling of effects of biological cropping from effects of removal of competition for energy.

Methods

REvoSim functionality

The Rapid Evolutionary Simulator (REvoSim) is an agent-based simulation tool, capable of modelling populations of hundreds of thousands of organisms over hundreds of thousands of generations within a spatially explicit, dynamic environment. REvoSim has been shown to reproduce real evolutionary trajectories (Garwood et al. 2019) and to be useful as a tool for testing existing eco-evolutionary hypotheses (Furness et al. 2021a, b).

The full operation of REvoSim, and its default conditions, are described in Garwood et al. (2019) and Furness et al. (2023), and full documentation is available from https://revosim.readthedocs.io/en/v3.0.1/. However, a summary is provided here for convenience, as are full details of minor changes made for the purposes of the experiments conducted in this study.

Individuals in REvoSim possess binary genomes (64 bits in length, by default) and exist in a space called a “slot”, within one of 10,000 “cells”, in a 100 × 100 cell square grid. Each cell has, by default, 100 slots, and each cell possesses three abstract environmental parameters, specified using the red, green, and blue colour channels of a 100 × 100 pixel image. Change over time in pixel colours can therefore be used to create change over time in environments. Organisms settle into a cell at birth and remain in that cell for the duration of their life. Organisms are assigned a "fitness" value that is determined by an interaction between their genome and the environmental parameters of their cell. A user-defined energy budget is provided to each cell in each timestep of the model (referred to as an "iteration"), and this energy is divided among all resident organisms proportional to their fitness. Genomes that are optimally fit in one environment are unlikely to be fit in another random environment, and small changes in environmental parameters result in small changes in organism fitness. The rate at which genome fitness decreases as genomes deviate from an optimum genotype is determined by a "settle tolerance" parameter. High values of the settle tolerance parameter result in reduced punishment of suboptimal genomes and represent a less steep fitness landscape.

By default, 100 genetically identical organisms, capable of surviving in the environment, are seeded into the central cell of the grid at the start of a simulation. Organisms with sufficient energy will expend that energy to attempt to breed. Attempting to breed consists of choosing another breeding organism in the same cell at random and, if the two organisms are sufficiently genetically similar, expending energy to produce an offspring organism. Offspring genomes are a mixture of the genomes of the two parents, with the exception that a mutation may sometimes occur, flipping the state of one bit in the offspring's genome. Offspring undergo dispersal, settling into either the same cell as their parents or a nearby cell, where they then begin their own life cycle. After a fixed number of iterations (default 15), organisms die. Dead organisms are removed from the simulation.

Mutation and selection for optimal fitness within the environmental conditions of a particular cell results in realistic biological evolution within organism genomes. Since different genomes are optimised for energy gathering in different environmental conditions, genomes of organisms will tend to differ between cells and will differ more between cells that differ more in their environmental conditions. Restricting the ability of organisms to breed based on the similarity of their genomes results in the formation of strictly genetically isolated groups, specialised to their local environmental conditions, that are algorithmically detected by the program and flagged as distinct species on the basis of the biological species concept (Mayr 1942).

REvoSim includes a variety of more complex features such as the ability to allow organisms to act as predators or to die early as a result of pathogens (Furness et al. 2023). These features are not employed in this study.

REvoSim adjustments

We made two small changes to the functioning of REvoSim in order to implement (a) biological cropping and (b) space limitation, within our experiments. Biological cropping was implemented by introducing code such that in every iteration after the first 100, every organism had an independent 30% chance of being assigned the maximum allowed organism age (such that it would die the next time its age was checked by the simulation). This change is functionally equivalent to introducing a high level of ecologically neutral predation pressure (i.e. cropping). A 100-iteration burn-in period with no cropping existed at the start of the simulations to allow for the establishment of a sizeable population before cropping began, to prevent stochastic population collapse. Space limitation was implemented by reducing the number of slots in each cell below what would otherwise be the equilibrium number of organisms present in that cell (in this case, from the default of 100 per cell to 8 per cell). However, this adjustment alone would have resulted in unrealistic behaviour since REvoSim, by default, iterates over cells in a fixed order while running simulations, and cells processed first would always fill all vacant slots in neighbouring cells, resulting in nonrandom migration of genomes through the simulated environment. Note that this phenomenon only occurs if cells are able to "fill up" all their slots; in normal usage, constraints of energy input prevent this from occurring. To prevent this artefact from arising in our simulations, we modified REvoSim to process cells in a random order in every iteration.

Simulations run

We ran 64 replicate simulations for each of 9 different combinations of simulation settings (Table 1). Simulations employed 128-bit organism genomes, with every bit of each genome applied to determine organism fitness and breeding compatibility. The use of 128-bit genomes, rather than the default 64-bit genomes, greatly increased the number of possible genomes that could exist. This was done to increase the absolute magnitude of any differences in genome diversity among experimental treatments. The "fitness target" parameter was adjusted to the recommended value for 128-bit genomes (i.e. a value of 264) in all simulations. When simulations terminated early due to the stochastic death of all organisms, these simulations were discarded from the final analysis.

Experiments labelled E are limited in organism abundance by energy input, and therefore encourage selective competition among individuals, as in a wide range of real-world ecosystems (e.g. waders competing for food resources on a mudflat; Vahl et al. 2005). Experiments labelled C are limited in organism abundance by biological cropping.

Table 1 Variable simulation settings employed in our experiments. The maximum genetic hamming distance for breeding (MaxD) refers to the maximum number of pairwise genetic differences between the genomes of prospective breeding partners where breeding is still possible. The fitness landscape flatness is the inverse of the rate at which the fitness of organisms declines as their genomes become progressively less well adapted to their environment. These 18 treatments are divided into three groups of six for the purposes of analysis

Experiment ID	Energy input	Maximum genetic hamming distance for breeding (MaxD)	Settle tolerance (fitness landscape flatness)	Biological cropping	Slots per cell
1.E	885	3	30	No	100
1.C	4000	3	30	Yes	100
1.S	4000	3	30	No	8
2.E	885	3	5	No	100
2.C	4000	3	5	Yes	100
2.S	4000	3	5	No	8
3.E	885	12	30	No	100
3.C	4000	12	30	Yes	100
3.S	4000	12	30	No	8

Experiments labelled S are limited in organism abundance by available space, as in some communities of sessile organisms (e.g. kelp; Reed 1990). Competition for space (S) and competition for energy (E) are not equivalent in REvoSim because only the latter is under genetic control within the simulations. Energy input settings in experiments labelled E, and slots per cell settings in experiments labelled S, were chosen in order to limit mean organism abundance in those experiments as closely as possible to the mean organism abundance in otherwise equivalent experiments with biological cropping (C), to minimise effects of organism abundance on genetic diversity (Table 1). Experiments 2 and 3 were conducted to determine the effect on the biological cropping mechanism of increasing the strength of competitive exclusion or decreasing the strength of homogenising sexual selection, respectively.

Simulations were run for 100,000 iterations each, using an environment image where all cells had identical environmental conditions, and environmental conditions did not change over time (i.e. a 100 × 100 image of a single colour). This environment was chosen so that genetic diversity generated by biological cropping was isolated from any genetic diversity that might otherwise arise as a result of adaptation to a diversity of local environmental conditions. Furthermore, this environment reflects the environmental conditions proposed for the deep sea in Dayton and Hessler (1972), where the biological cropping hypothesis is invoked as a potential explanation for high diversity.

Genetic diversity (i.e. the number of unique genomes) and total organism abundance were measured in the last iteration of each simulation. Although the biological cropping hypothesis, as originally formulated, is concerned with species diversity rather than genetic diversity, the two are affected by the same drivers (Evanno et al. 2009), and measuring genetic diversity removes complexity related to species concepts (Hey 2006). Mean genetic diversity was compared among simulations to determine the effects of biological cropping and space limitation under different genetic and fitness landscape conditions.

Results

Of the 576 simulations run, 45 were terminated early due to the stochastic death of all organisms. These simulations are excluded from the statistical analysis. The lowest number of simulation replicates completed for any one experimental treatment was 44. The effect of biological cropping and space limitation on genetic diversity varied depending on both the maximum genetic hamming distance over which breeding was possible (MaxD), and the settle tolerance (Fig. 1). Under initial MaxD and settle tolerance settings (experiment 1; Fig. 1a), biological cropping had a significant negative impact on genetic diversity (t-test: $t = -6.0014$, $p = 2.538 \times 10^{-7}$, difference in means = 713 = 13.0% of genetic diversity absent cropping).

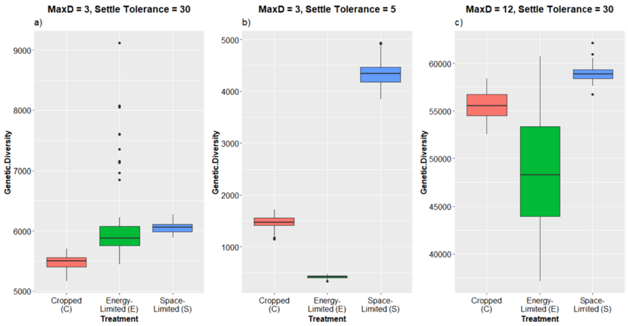

Fig. 1 Genetic diversity (i.e. number of unique genomes) in **a** experiment 1, **b** experiment 2, and **c** experiment 3. The number of individuals is similar in each treatment and, therefore, cannot have a substantial confounding effect on the observed genetic diversity

The impact of space limitation on genetic diversity was not significantly negative (*t*-test: $t = -1.2386$, $p = 0.2217$, difference in means = 146 = 2.3% of genetic diversity absent cropping). When settle tolerance was lower (experiment 2; Fig. 1b), both biological cropping and space limitation had significant positive impacts on genetic diversity (*t*-tests: biological cropping: $t = 63.141$, $p < 2.2 \times 10^{-16}$, difference in means = 1044.6 = 249.2% of genetic diversity absent cropping; space limitation: $t = 125.76$, $p < 2.2 \times 10^{-16}$, difference in means = 3917.0 = 934.3% of genetic diversity absent cropping). The same was true when MaxD was higher (experiment 3; Fig. 1c), when both biological cropping and space limitation had significant positive impacts on genetic diversity (*t*-tests: biological cropping: $t = 7.895$, $p = 3.743 \times 10^{-10}$, difference in means = 7358 = 15.3% of genetic diversity absent cropping; space limitation: $t = 11.642$, $p = 4.58 \times 10^{-15}$, difference in means = 10,695 = 22.2% of genetic diversity absent cropping). Equilibrium species diversity was one in all simulations.

Discussion

Statistical analysis of simulated datasets

We conducted frequentist statistical analysis of our simulation outputs. White et al. (2014) objected to the use of frequentist statistics on simulated data on two grounds. Firstly, on the basis that simulations can be replicated intensively, such that very small effect sizes can become statistically significant while being biologically meaningless; and secondly, on the basis that simulations with different priors violate *a priori* the null hypothesis that different treatments do not differ. However, the first objection can be applied equally to any large dataset, be it derived from simulations, observations, or real-world experiments. Furthermore, the existence of non-significant statistical results in our analyses (experiment 1) suggests that over-replication was not an issue. The second objection can also be applied equally to simulation experiments and real-world experiments, since the prior conditions of the experiment must differ between treatments in both cases. Nevertheless, we report effect sizes (difference in genetic diversity between treatments as a percentage of the genetic diversity in the uncropped treatment) in addition to statistical results (*p*-value and *t*-value) to alleviate any concerns over the application of frequentist statistics to simulation results.

The biological cropping hypothesis

The simulations conducted here demonstrate that biological cropping can, under certain conditions, be sufficient to significantly increase the equilibrium genetic diversity of populations over evolutionary timescales (Fig. 1b, c). This is a novel finding, which matches the predictions of the biological cropping hypothesis (Dayton and Hessler 1972). On the other hand, our simulations also demonstrate that, under other conditions, biological cropping can significantly *reduce* the equilibrium genetic diversity of populations (Fig. 1a). This is contrary to the predictions of the biological cropping hypothesis (Dayton and Hessler 1972) and cannot be explained as a prediction of the more-individuals hypothesis (Storch et al. 2018), since experimental design ensured that cropped and uncropped ecosystems contained similar numbers of individuals. We hypothesise that this is the result of sexual selection: since organisms in intensely cropped ecosystems are at a high risk of dying, they are under strong selective pressure to breed as soon as possible. The less common an organism's genome, the greater the risk that it will fail to breed at any given attempt due to genetic incompatibility with its potential partner (see "Methods"). Consequently, biological cropping imposes positive frequency-dependent selection on organisms' genomes, reducing genetic diversity.

If this hypothesis is correct, then the net effect of biological cropping on genetic diversity within populations will be determined by the relative strengths of its opposing effects on competitive exclusion and sexual selection. If, in the absence of biological cropping, competitive exclusion is strong compared to sexual selection, then the commencement of biological cropping in the ecosystem should *increase* genetic diversity. Conversely, if, in the absence of biological cropping, competitive exclusion is weak compared to sexual selection, then any biological cropping should *decrease* genetic diversity. This hypothesis is supported by our simulation results: under the conditions of experiment 1, biological cropping has a net negative effect on genetic diversity (Fig. 1a). However, when competitive exclusion is strengthened by increasing the steepness of the fitness landscape (experiment 2), or sexual selection is weakened by increasing the threshold number of pairwise genetic differences between organisms required for breed failure to occur (experiment 3), the net effect of biological cropping on genetic diversity becomes positive (Fig. 1b, c).

The results of our space-limited simulations provide further support for this hypothesis. Space limitation in REvoSim reduces selection on the ability to compete for energy resources in the same way as cropping, by reducing the number of organisms in the environment. However, unlike biological cropping, it does this without imposing on organisms a risk of premature death. Consequently, space limitation replicates the positive effects of biological cropping on genetic diversity without replicating the negative effects. As a result, genetic diversity in space-limited simulations is never significantly lower than genetic diversity in other simulations of equivalent population size, and sometimes significantly higher (Fig. 1). This accords with observational studies that have shown that space limitation results in the maintenance of population genetic structure in taxa that would otherwise be expected to experience significant homogenising gene flow between populations (Orsini et al. 2013; Vaux et al. 2022).

Our results suggest that the positive effects of biological cropping on diversity are contingent upon cropping relieving organisms' genomes of the effects of selection pressure, since response to selection pressure will result in loss of less fit genes (and therefore diversity) from the gene pool (Brisson 2018). This is consistent with the analysis by Gooch and Schopf (1972), which concluded that higher than expected genetic variability in the deep sea could be explained if organisms' genomes contained a higher than average concentration of neutral genetic polymorphisms. Consequently, the positive effect of space limitation on genetic diversity that we observe is likely contingent upon the ability to compete for space not being under genetic control, and hence not responding to selection pressure. If competition for space was under genetic control, then space-limited simulations would simply replace selection for ability to compete for energy resources with selection for ability to compete for space, with no alleviation of the net selection pressure on organisms' genomes. In the context of the biological cropping hypothesis, this means that, in order for cropping to increase equilibrium diversity, organisms must be limited in their ability to respond to selection pressure imposed by the cropping predators.

In scenarios where a prey population's capacity for predator avoidance is under selection, culling of unfit organisms will swamp any positive effects of cropping on diversity. This will apply if selection for predator avoidance is resulting in continuous evolutionary change (e.g. Red Queen dynamics; Van Valen 1973). However, it will also apply if the prey population's predator avoidance strategy is optimal, and selection is only acting to remove unfit novel phenotypes from the population. In contrast, negative frequency-dependent selection on prey is likely to increase diversity whenever it occurs by favouring rare phenotypes even if they would otherwise be selected against (Gendron 1987). Negative frequency-dependent selection is not likely to occur in all ecosystems (Briggs 1985), but where it does occur it could, in theory, operate in tandem with biological cropping to increase diversity. However, negative frequency-dependent selection requires that some phenotypes be selected for and others selected against and, as such, is liable to impose selection pressure on populations. If those populations can respond to such pressure through evolution, then the positive effects of biological cropping on diversity will be replaced by the effects of negative frequency-dependent selection.

Our simulations lay out the theoretical circumstances under which biological cropping might be expected to elevate the equilibrium genetic diversity of ecosystems. However, whether or not this actually occurs within real-world ecosystems remains an open question (McClain and Schlacher 2015; Paulus 2021). It has been argued that the biological cropping hypothesis is not an appropriate explanation for higher than expected diversity in deep marine benthic ecosystems because the life histories of organisms in those ecosystems cannot support high mortality rates (Grassle and Sanders 1973; Gage 1996), although this is not certain (Williamson 1977). Furthermore, it is not clear whether organisms in cropped ecosystems would generally be able to adapt under intense selection pressure to reduce predation mortality. Our simulations suggest that an inability to undergo such adaptation would be a prerequisite for the operation of the biological cropping hypothesis. In the case of the deep marine benthos — the environment in the context of which the biological cropping hypothesis is most often discussed (Dayton and Hessler 1972) — it is not even certain that diversity is actually unusually high (McClain and Schlacher 2015). The elevated diversity of the deep marine realm is often cited as an unusual eco-evolutionary phenomenon, requiring explanation (Gooch and Schopf 1972; White 1988; Gage 1996), but empirical datasets are sparse (Gray et al. 1997), and empirical analyses of the shape of the diversity-depth relationship have produced mixed results (Smith and Brown 2002; Olabarria 2006; Bridges et al. 2022). Further empirical study of the diversity and structure of deep-sea ecosystems, and the life-histories of their inhabitants, is therefore required to determine to what degree these ecosystems meet the theoretical requirements for biological cropping to play a role in influencing their diversity.

Conclusions

These simulations provide the first in silico evidence that nonselective biological cropping can increase the equilibrium genetic diversity of ecosystems over evolutionary timescales. However, this effect is contingent upon biological cropping reducing the selection pressure operating on organisms' genomes: a condition that may not be met if the intense predation inherent to the cropping process produces new selection pressures to which organisms can respond, such as selection for predator avoidance or defences or selection for rapid and reliable reproduction. This result provides a framework within which the potential for biological cropping to drive diversity increases in the real world can be evaluated and further demonstrates the utility of individual-based simulations as tools to answer eco-evolutionary questions. However, further observational study of real-world ecosystems, particularly the deep marine benthos, is required in order to determine the importance of biological cropping as a driver of biodiversity in the real world.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12080-024-00579-3.

Author contribution Euan Furness: conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing—original draft, visualisation; Mark Sutton: software, validation, resources, writing—review and editing, supervision, project administration, funding acquisition.

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Code and data availability The code for REvoSim, including all changes made to that code to introduce the cropping and random cell access order features in this study, is freely available from GitHub: https://github.com/palaeoware/revosim. Genetic diversity and population size measurements derived from experiments in this study are available in the supplementary information.

Declarations

Competing interests The authors declare no competing interests.

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