Palaeontology The Palaeontological Association www.palass.org

[Palaeontology, Vol. 67, Part 5, 2024, e12701]

Exploring the macroevolutionary impact of ecosystem engineers using an individual-based eco-evolutionary simulation

by THOMAS J. SMITH[1]*, LUKE A. PARRY[1], FRANCES S. DUNN[2] *and* RUSSELL J. GARWOOD[3,4]*

[1]Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK; thomas.smith@earth.ox.ac.uk
[2]Oxford University Museum of Natural History, University of Oxford, Parks Road, Oxford OX1 3PW, UK
[3]Department of Earth and Environmental Sciences, University of Manchester, Manchester M13 9PL, UK; russell.garwood@manchester.ac.uk
[4]Natural History Museum, London SW7 5BD, UK
*Corresponding author

Typescript received 15 December 2023; accepted in revised form 19 April 2024

Abstract: Ecosystem engineers can radically reshape ecosystems by modulating the availability of resources to other organisms through modifying either physical or biological aspects of the environment. The introduction or removal of ecosystem engineers from otherwise stable ecosystems can impact the diversity of co-occurring species, such as driving local extinctions of native taxa. While these impacts are well established over ecological timescales for a wealth of taxa, the macroevolutionary implications of the onset of ecosystem engineering behaviours are less clear. Despite this uncertainty, ecosystem engineering has been implicated in several major transitions in Earth history including the appearance of extensive bioturbation during the Cambrian substrate revolution and associated Ediacaran–Cambrian turnover, and the Great Oxygenation Event. Whether ecosystem engineers are frequently associated with turnover and extinction in deep time is not known. Here we investigate this with an eco-evolutionary simulation framework in which we assign lineages the ability to impact the fitness of co-occurring taxa through phenotype–environment feedback. We explore numerous conditions, including how frequently such feedback occurs, and whether ecosystem engineers modify or create niches. We show that there is no general expected outcome from the introduction of ecosystem engineers. In a minority of runs, ecosystem engineering lineages completely dominate, rendering all others extinct, but in others they persist (but do not dominate), or die out. We suggest that ecosystem engineers have complex impacts, but possess the capacity to profoundly shape diversity, and it is appropriate to consider them alongside other exogenous extinction drivers in deep time.

Key words: macroevolution, ecosystem engineering, simulation, modelling, ecology, Cambrian–Ediacaran transition.

FEEDBACK between organisms and their environment occurs over a wide range of spatial and temporal scales, with myriad consequences for other organisms and the environments in which they live. Ecosystem engineers alter the resources available to other organisms by changing either biotic (excluding trophic interactions) or abiotic factors, and as a consequence modify, create, maintain or (when introduced or invasive) destroy habitats (Jones *et al.* 1994). While a common impact of ecosystem engineers is the restructuring of communities when they are present or removed, they may also profoundly change the abiotic environment. Some of these impacts may persist over incredibly long timescales, such as deep-time changes to biogeochemical cycling, the ventilation of the oceans, or the composition of the atmosphere (Butterfield 2011). This variety reflects the diversity of habitat-altering behaviours exhibited by modern animals and other organisms, although it is debated whether they all constitute ecosystem engineers (Jones *et al.* 1994) or just those that change the abiotic environment (Hastings *et al.* 2007).

The introduction of ecosystem engineers as invasive species or their removal (such as through human overexploitation) clearly illustrates the impact that they have on environments, often with devastating consequences. The introduction of invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels into the Great Lakes of North America (the largest freshwater ecosystem in the world) has devastated native benthic species, outcompeting native bivalves for food and smothering the benthos as a consequence of their ability to attach to a range of substrates (Ricciardi *et al.* 1997; Beekey *et al.* 2004). Beyond changing the makeup of communities, the ability of these species to efficiently filter water has also changed the biogeochemical profile of the Lakes by, for example, modifying the phosphorus cycle (Li *et al.*

doi: 10.1111/pala.12701

2021). Ecosystem engineers can be placed into two broad classes: autogenic engineers change an aspect of themselves or their own structure that in turn modifies an environment (e.g. accumulations of zebra and quagga mussels smother the benthos) and allogenic engineers change the environment from one physical state to another (e.g. construction of beaver dams) (Jones *et al.* 1994).

Despite the ubiquity of ecosystem engineering in modern ecosystems, there are few examples of events in deep time where biotic turnovers or persistent changes to Earth's environment can be linked to the evolution of novel ecosystem engineering behaviours. However, where the appearance of major engineering behaviours can be identified in the fossil record, these are associated with profound global changes. The evolution of reef systems are a key example; reefs appear independently in at least four animal phyla (sponges, cnidarians, annelids, molluscs), with many independent gains and losses of the reefal habit within these groups (e.g. tabulate, scleractinian and octocoral cnidarians). Through deep time, this has resulted in a boom and bust pattern of reef diversity, including long durations with no reef ecosystems, resulting in fluctuations in the impact of reef engineering properties through geological time, including changes to carbon cycling (Wood 1993). Other examples of ecosystem engineering in deep time have resulted in permanent state changes to the biosphere. The Great Oxygenation Event, which resulted in a fundamental shift in the composition of Earth's atmosphere, is associated with the evolution of photosystems in cyanobacteria (Schirrmeister *et al.* 2015). The appearance of deep-rooting systems in early plants stabilized banks, and resulted in fundamental changes in the geomorphology of river systems; prior to this point, meandering systems were far less widespread (McMahon & Davies 2018). Another example of a critical turning point in Earth history is the Ediacaran–Cambrian transition, during which the appearance and diversification of the major animal lineages, and their associated novel engineering behaviours, coincided with the extinction of the Ediacaran macrobiota (Mussini & Dunn 2023). Burrowing, pumping and swimming changed the world, altering biogeochemical cycling (e.g. Van de Velde *et al.* 2018), ventilating the oceans, and disturbing the dominant mat-ground benthic environments (Butterfield 2017). The broadly coeval appearance of these ecosystem engineering behaviours and the extinction of the Ediacaran macrobiota has led to the suggestion that the two are linked and that ecosystem engineering behaviours drove the decline and fall of the Ediacarans (Laflamme *et al.* 2013; Darroch *et al.* 2015, 2018). Conversely, some have suggested that biodiversity loss at the end-Ediacaran is comparable to that at a traditional mass extinction boundary (e.g. Darroch *et al.* 2015), and have invoked abiotic environmental change to explain it as with all of the traditional 'Big 5' extinctions (Evans *et al.* 2022). Notably, however, there is no 'smoking gun' for any abiotic driver in this case (see Mussini & Dunn 2023). If the extinction of the Ediacarans was driven by evolving organisms engineering their environment, it would represent an event without comparison in the subsequent half a billion years.

Ecosystem engineering behaviours can profoundly change environments, selective pressures, and, ultimately, evolutionary trajectory. However, it is not clear whether the origin of these behaviours can produce concurrent short term, large scale biodiversity losses, comparable to the major abiotic drivers of mass extinctions (e.g. volcanism). To address this, we have performed a series of individual-based eco-evolutionary simulations with varying implementations of organism–environment feedback. Our system is abstract and thus compatible with any definition of 'ecosystem engineering' (e.g. Jones *et al.* 1994; Reichman & Seabloom 2002; Wilby 2002; Hastings *et al.* 2007), and we use our experiments to explore general outcomes from the evolution of novel, environment modifying behaviours.

MATERIAL AND METHOD

Simulation framework

For this study, we have used TREvoSim v3.0.0 (Keating *et al.* 2020; Garwood *et al.* 2024) to generate phylogenies, character matrices, and data on environmental engineers (a graphical summary of the procedure is shown in Fig. 1). TREvoSim is an individual-based model and software implementation that includes competition and natural selection, a species definition, and from v3.0.0, an ecosystem engineering system. A full overview of the model is provided in Keating *et al.* (2020, v1.0.0) and Mogniardino Koch *et al.* (2021, v2.0.0). In brief, the simulation employs digital organisms composed of a user-defined number of binary characters. These are placed in a playing field: a list of organisms whose fitness is calculated using one or more environments (a user-defined number of random binary strings, by default the same length as the organism genomes). Fitness is calculated based on genomic distance from these environmental numbers (masks), and the simulation allows multiple playing fields if desired, each with its own environment(s). The simulation is seeded with a single genome and, as it iterates, fitter organisms are more likely to be selected for asexual replication with a user-defined chance of mutation. Species, defined by genomic distance from the parent lineage, appear and ultimately go extinct, and the environment mutates.

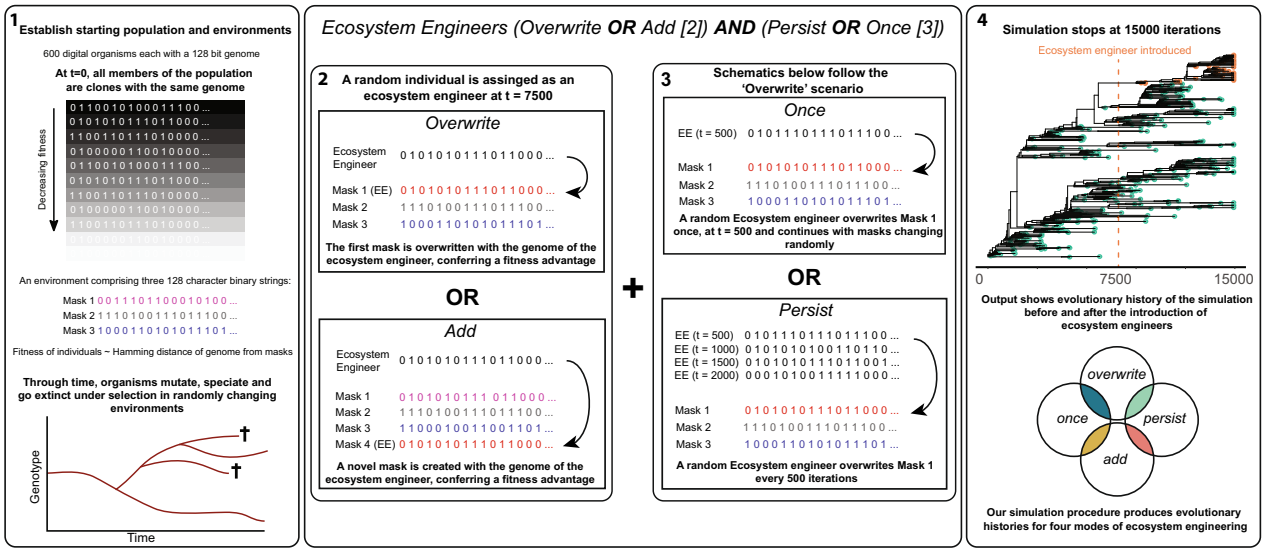


FIG. 1. The TREvoSim v3.0.0 simulation pipeline used for the current study. Within the individual-based simulation, organisms speciate and go extinct. Ecosystem engineering is applied halfway through the simulation and the ecosystem engineer's genome is either used to overwrite one of the masks in each environment of every playing field, or is added as a mask to every environment of every playing field. This happens either once, or repeatedly at every 500th iteration until the simulation terminates. The colours used in the Venn diagram in box 4 are used throughout the main text figures to denote simulation parameters.

Here we use a newly added ecosystem engineering system to study the impact this has during simulations (Fig. 1). This is first applied halfway through a simulation (at either half the requested number of iterations, or half the requested number of species): a random individual from a playing field is selected as an ecosystem engineer (EE) and they are assigned ecosystem engineering status, which they pass on to all their descendants. The genome of an EE is either:

1. Used to overwrite the first mask for every environment across all playing fields, or
2. Used as the basis of a new mask that is added to every environment, across all playing fields.

EEs are either:

1. Applied just once, and then the simulation is run to the requested number of iterations or species, or
2. If requested, run repeatedly, with a user-defined frequency (which we have termed persistent ecosystem engineering). For ecosystem engineering applications after the first, a random individual from within the pool of EEs is chosen as the source of the overwritten mask (either the previously overwritten mask or the added one: when a mask is added, this only occurs once at initial EE application).

In all of these scenarios, the similarity between the genome of the EE and the mask provides EEs with an advantage by improving their fitness, consequently improving their likelihood of selection for replication (but not guaranteeing they will replicate).

Simulation parameters

We ran simulations for 15 000 iterations, using 128 bit organisms. Each playing field was associated with three environments, each comprising three masks. Runs included a single playing field of 500 organisms and our experiments comprised 1000 repeats of the following:

1. Baseline runs without EEs
2. Applying EEs once, halfway through the simulation
3. Applying EEs halfway through the simulation, then every 500 iterations subsequently.

For each replicate we output:

1. The phylogenetic tree of all species during the run
2. A CSV outlining the ecosystem engineering state of each species at the end of the simulation
3. A phylogenetic matrix with all species genomes at the termination of the simulation
4. For every iteration in which EEs were applied, a file documenting the playing field state, selected EE, and the environments.

The remaining simulation parameters are provided in Table 1.

Analytical pipeline

All analyses were conducted in R (R Core Team 2023). For each repeat of every experiment including EEs, we used a modified version of the ape ltt.plot.coords function (Paradis

TABLE 1. TREvoSim simulation parameters.

Variable	Value
Genome size/species select size/fitness size	128
Run for (iterations)	15 000
Species difference	10
Environment mutation rate	1
Organism mutation rate	1
Environment number	3
Mask number	3
Selection level	2
Fitness target	0
Unresolvable cut-off	5
Stochastic layer	False
Random overwrite	False
Strip uninformative	False
Match fitness peaks	False
Expanding playing fields	False

& Schliep 2019) to track how the number of lineages designated as EEs changed through time (Fig. 2). We also randomly selected a non-EE lineage present at the halfway point of each experiment (iteration 7500 of 15 000), baseline runs included, and tracked how its descendants changed in number through time for comparison. Using these data, we determined two outcomes: whether the descendants of the EE or the chosen non-EE lineage survived until the end of the simulation, and whether they came to account for all lineages in it (an outcome we hereafter refer to as 'domination'). The proportion of repeats in which these outcomes occur and the number of species present at the end of each repeat were then summarized for each experiment.

These lineage-through-time data were then decomposed into their constituent lineage origination and extinction data, from which estimates of rate were derived. These data were partitioned into 10 iteration time bins sampled at 5 iteration intervals; bin $n + 1$ samples the last 5 iterations of bin n and the 5 iterations that follow, bin $n + 2$ the last 5 iterations of bin $n + 1$ and the next 5 iterations, and so on. Per-iteration rate estimates were derived for EEs and non-EEs by dividing the number of origination and extinction events occurring within each bin of each by 10. These were then corrected for differences in standing richness between EEs and non-EEs by dividing each estimate by the mean number of EE and non-EE lineages present across each time bin. The mean and standard deviation for each time bin of rate estimates were then derived to facilitate visualization.

RESULTS

In all our experiments, regardless of simulation parameters: EE takeover is not inevitable (Fig. 3); EEs do not always persist to the end of the simulation; and the introduction of EEs reduces the proportion of non-engineering lineages that persist to the end of simulations. These general patterns are recovered regardless of whether EE status is used to overwrite a mask, or whether it is used to add a mask to the environments. When ecosystem engineers are applied once during a run, in either formulation of EEs, this lineage has a slightly increased probability of surviving to the end of a simulation compared to a randomly chosen lineage in a baseline run, at the expense of the survival of the non-engineers.

A similar pattern with slightly higher magnitude is present in the proportion of lineages that go on to dominate the simulation. In both cases, however, absolute values of dominance and survival remain low when ecosystem engineers are applied once, and dominance is slightly more pronounced when ecosystems overwrite, rather than add, a mask. This pattern is amplified further when ecosystem engineers are persistent; in more than half our replicates with persistent ecosystem engineers, these go on to dominate the simulation, whilst the same is true of a very small proportion of non-engineering lineages, and the proportion of EE dominance is higher when a mask is overwritten relative to when one is added.

Speciation and extinction through time plots demonstrate that these processes remain constant throughout our baseline runs (see Figs S1–S6) and in our other simulations prior to the introduction of EEs (Fig. 4). Similarly, when ecosystem engineers are applied just once, speciation and extinction rates in non-EE lineages remain constant throughout the second half of the run regardless of the formulation of ecosystem engineering used, albeit with a short period of depressed speciation and heightened extinction immediately after the application of EEs. In runs in which ecosystem engineers are applied just once, there is a peak in EE speciation at their application, with a long asymptotic tail as the simulation progresses (Fig. 4A). This is followed by a gradual increase in extinction in EE lineages (Fig. 4B), which gently peaks *c.* 1000 iterations after their application before declining towards the end of the simulation. When ecosystem engineering is persistently applied after initially adding or overwriting a mask, we see peaks in speciation (Fig. 4C) and troughs in extinction (Fig. 4D) in EE lineages in association with each engineering event. The speciation peaks reduce in amplitude as the simulation progresses, presumably as an increasing proportion of the runs are dominated by ecosystem engineers. Also associated with the persistent application of ecosystem engineers, we observe reduced speciation and increased extinction (Fig. 4E, F) in the non-EE lineages regardless of whether a mask was originally added or overwritten.

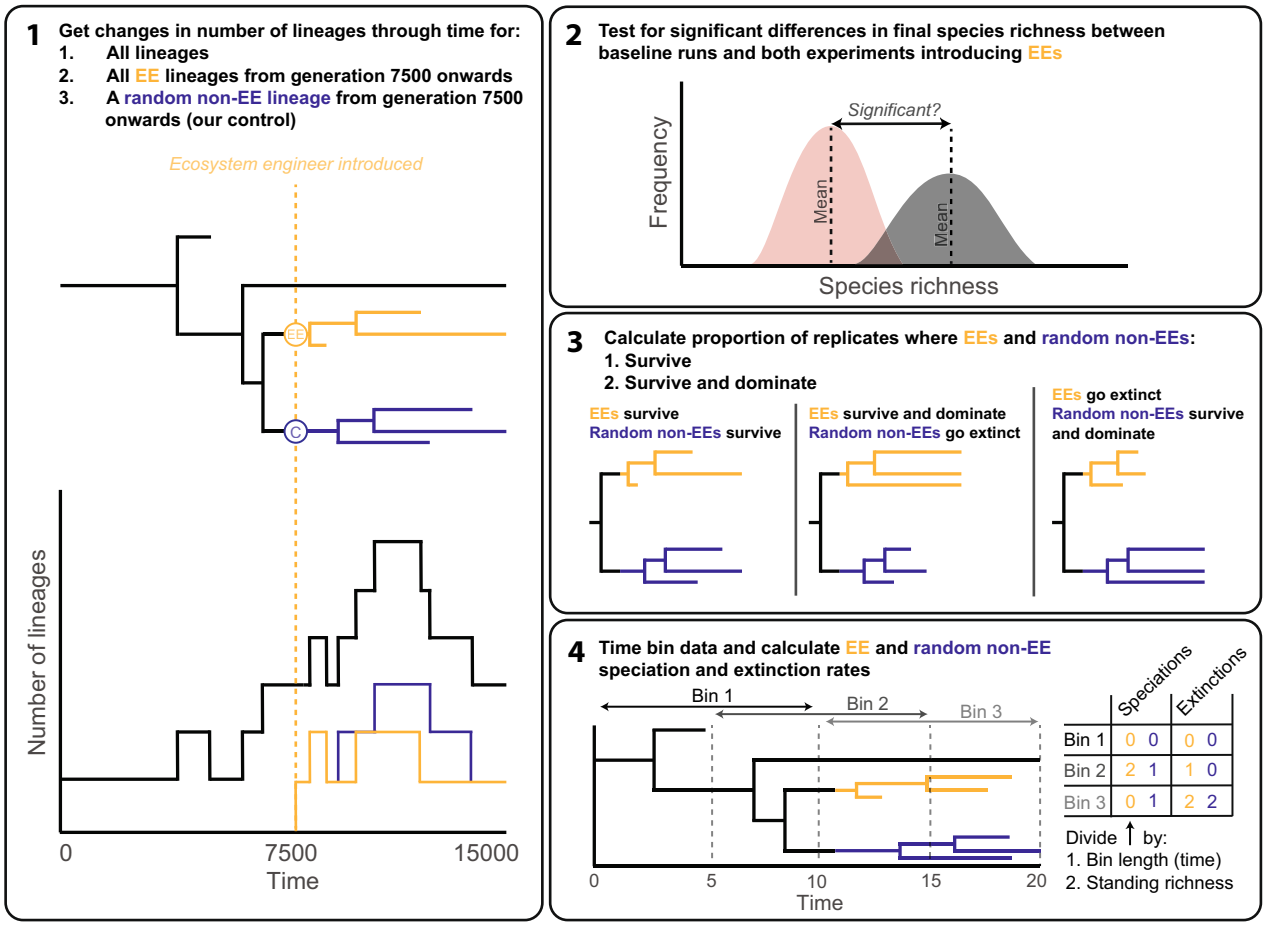
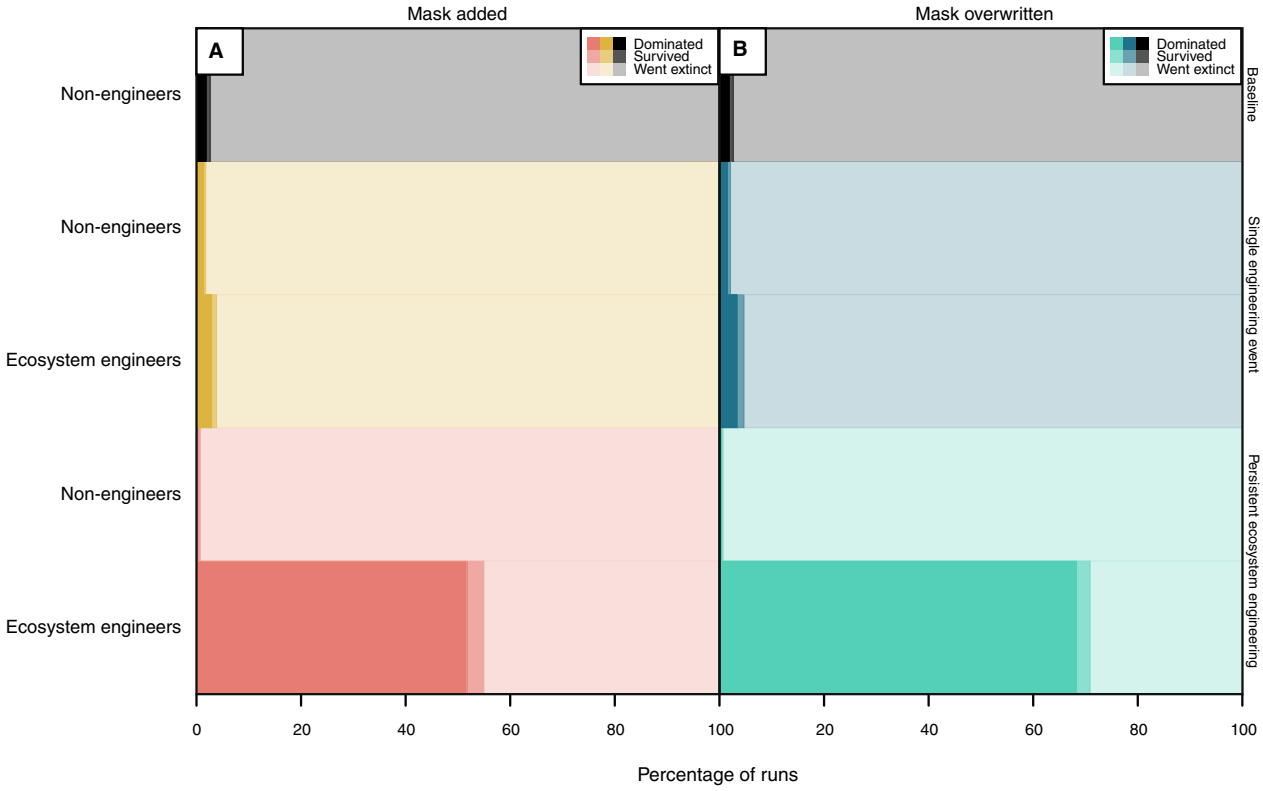


FIG. 2. The analytical pipeline used for the current study. Lineage-through-time data were collected for all lineages, lineages designated as ecosystem engineers, and a randomly selected non-EE lineage present at the halfway point of the simulation. Student's *t*-test was used to test for significant differences between the final species richness of the baseline runs and those simulations applying ecosystem engineering. These data also allowed us to compare the proportion of replicates in which EE lineages and the randomly selected non-EE lineages survived until the end and went on to account for 100% of the surviving lineages between simulations. We refer to this second result as 'domination' throughout this paper. Finally, we binned our lineages into 10-iteration bins separated by 5-iteration increments (i.e. each bin overlaps with each preceding and succeeding bin) and counted the number of EE and random non-EE speciation and extinction events. These data were then converted into estimates of per-iteration rate by dividing them by the length of the bin they were sampled in (i.e. time elapsed), and then to per-iteration, per-lineage rates by dividing the result by mean number of relevant lineages present across the bin.

DISCUSSION

Through our simulations, we quantify the general impacts of the introduction of ecosystem engineers to previously stable environments and observe a range of possible outcomes. These include instances where EEs completely dominate by the end of the simulations, alongside cases where the impacts of EEs are ephemeral and they are rendered extinct after they originate. However, across all of our simulation conditions, EEs survive to the end of simulations more often than would be expected based on comparison with our baseline simulations, demonstrating that even when positive organism–environment feedback is enforced only once at a single time step, this confers a selective advantage, the impact of which persists for the duration of the simulation. We note two caveats here: our simulations are highly abstracted and do not integrate any form of mutualistic interactions between species; and we assume maximal benefit of the engineering behaviour for the engineer. Our conclusions, therefore, represent a first attempt at addressing this question and we set out future directions at the end of this contribution. Our results are consistent with ecological inheritance (Odling-Smee 1988) whereby organisms leave a legacy of selective pressures through ecosystem engineering activities for ecological and/or genetic descendants, thus



C

	Baseline	Mask added				Mask overwritten			
		Single engineering event		Persistent ecosystem engineering		Single engineering event		Persistent ecosystem engineering	
	Non-engineers	Non-engineers	Ecosystem engineers	Non-engineers	Ecosystem engineers	Non-engineers	Ecosystem engineers	Non-engineers	Ecosystem engineers
Dominated	1.9	1.4	2.9	0.4	51.7	1.6	3.4	0.4	68.3
Survived	0.7	0.4	1.9	0.3	3.3	0.5	1.3	0.3	2.6
Went extinct	97.4	98.2	96.1	99.3	45.0	97.9	95.3	99.3	29.1

FIG. 3. The percentage of 1000 runs in which the lineage designated as the ecosystem engineer or a non-engineering lineage randomly chosen at the halfway point of the simulation went extinct, survived until the end of simulation, or survived until the end of the simulation and accounted for 100% of the remaining lineages. Outcomes are presented as bar charts for the runs in which ecosystem engineering was not applied (top), ecosystem engineering was applied once (middle), and ecosystem engineering was applied repeatedly throughout the remainder of the simulation (bottom), the latter two for both formulations of ecosystem engineering: A, mask added; B, mask overwritten. These outcomes are also presented as raw percentages (C).

modifying their own evolutionary trajectories (e.g. Hastings *et al.* 2007). Survival of non-engineer lineages is suppressed to levels below the baseline when EEs are introduced, suggesting a general fitness disadvantage is conferred to non-engineering lineages.

Adding an environmental mask does not create novel ecospace in the same way that the evolution of reef-building (Wood 2001) and burrowing behaviours (Erwin 2008; Erwin & Tweedt 2012; Cribb *et al.* 2019) do in real biological systems. However, it does make the environment defined by the simulation parameters more complex. In contrast, overwriting a mask abruptly changes the environment it partially defines, but does not increase its complexity. Where masks are overwritten rather than added, the impacts on both EEs and non-engineers are more pronounced, with a higher proportion of replicates seeing EEs dominate. In simulations where a new mask is added and the environment made more complex, EEs persist to the end of the simulation less frequently, and dominate fewer replicates. This is

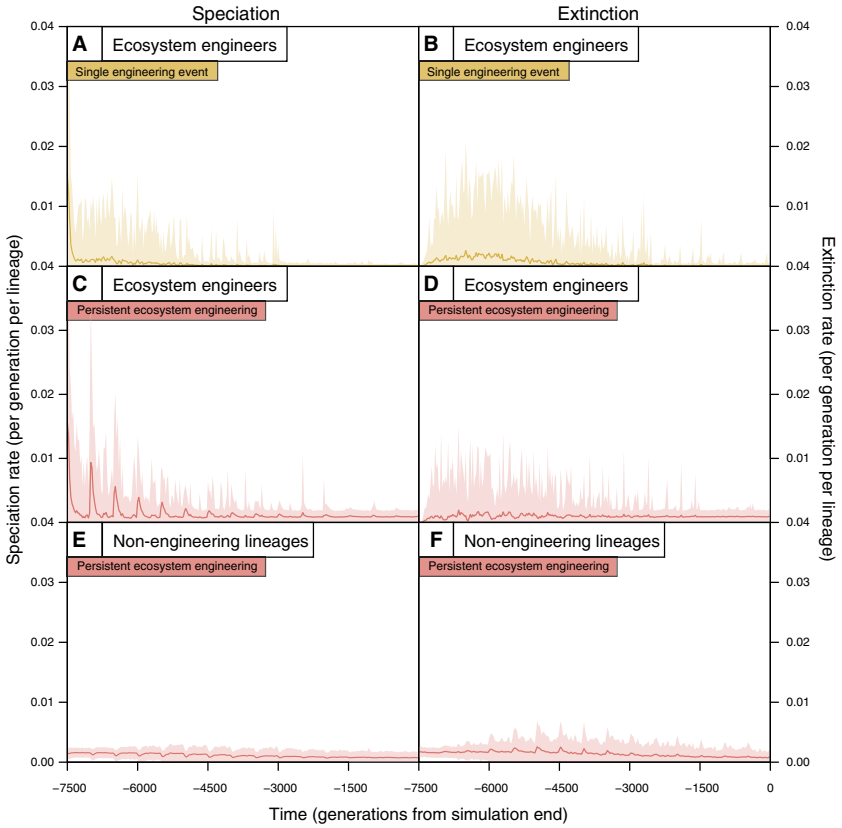


FIG. 4. Changes in mean EE (A–D) and non-EE (E, F) speciation (A, C, E) and extinction (B, D, F) rate through time after EEs were applied once (A, B) and persistently (C–F) through the addition of a mask. The dark lines represent the mean rates, while the pale silhouettes represent the rates that fall within one standard deviation (±) of the mean for each time bin. There were no meaningful differences between the changes in rate induced by applying EEs through the addition of a new mask or the overwriting of an existing one, hence we only present the results of the former here. Furthermore, as the speciation and extinction rates of non-EEs throughout our baseline runs and after EEs were applied once were effectively static, we do not present these results here. These results and all others are illustrated in Figures S1–S6.

probably because, when introduced, they do not overwrite a mask to which the existing inhabitants are well adapted. As such, the fitness of non-engineers is less substantially reduced.

The greatest factor in whether engineers rise to dominate is whether they modify an environment just once or if their feedback on the environment is introduced persistently and periodically. In the single-event simulation, EEs dominate 2.9–3.4% of simulations, depending on whether environmental masks are overwritten or created by engineers, whereas in the persistent simulation EEs dominate 51.7–68.3% of the time. Ecosystem engineering therefore exhibits the strongest impact on the ultimate taxonomic makeup and the evolutionary fate of simulations where its effects are continuous through time.

Where EEs go on to dominate simulations, the underlying mechanisms driving this takeover are manifest in our plots of speciation and extinction rates through time, and clearest in conditions where EE feedback to the environment is implemented at regular intervals. This feedback enhances speciation and depresses extinction in the EEs, and has the opposite effect on non-engineering lineages. This demonstrates that ecosystem engineering confers a fitness advantage to engineers, but also a concomitant reduced fitness to non-engineers. These opposite changes interact to increase the proportion of cases where EEs dominate by the end of the simulation; in other words, they drive a faunal turnover. Even when an EE is introduced only once, there is substantial variability to extinction and speciation rates through time compared with the baseline analyses (which show constant rates throughout the simulation), suggesting that even in this much more limited case, the introduction of feedback between organisms and their environments causes considerable instability. That these data confirm the capacity for long-term evolutionary consequences of single-event EE behaviour is concerning when considering the rising number of invasive or alien species being detected worldwide (IPBES 2023), suggesting a protracted impact even after rapid extirpation of invaders is possible, although it

is important to note that there is no measurement of absolute time in TREvoSim. Detailed work has tended to focus specifically on the impacts of alien species once they become invasive (i.e. established) but our data suggest that assessments of the potential for ecological inheritance in alien species regardless of long-term establishment may be required. This feeds into recently published work by Albertson *et al.* (2022) who proposed a framework to assess legacy effects of EEs based on residency time and body size, with explicit predictions about which scenarios will result in more protracted legacies. Such work may prove fruitful in informing conservation priorities.

The nature of our simulation does not allow us to comment about whether EEs are likely to impact overall species diversity in the real world. Some authors have suggested that positive feedback between life and environment resulting in niche construction (closely aligned with the idea of autogenic EEs) begets further niche construction and thus diversity (e.g. Erwin 2008) but within our simulation the primary control on species carrying capacity is the playing field size. For a playing field of a given size, carrying capacity could, in theory, vary if some formulation of ecosystem engineering introduced changes to the environment that allowed for more compact niches and more species represented by fewer individuals. However, this theory requires further testing.

Our plots of extinction and speciation rates through time show a fundamental change in state with the introduction of ecosystem engineers. Such a state change has been invoked to explain differences in the fossil record before and after the Ediacaran–Cambrian transition (Butterfield 2011). In this event, the origin of behaviours like burrowing, predation and the colonization of the water column by emergent ecosystem engineering animals are hypothesized to have radically modified the biosphere by changing biogeochemical profiles, and ventilating the oceans. Evolving animals are thought to have changed macroevolutionary trajectories, elevating extinction rates and decreasing taxon longevities, the former of which, at least, is recapitulated by our simulations. This disruption was accompanied by a major faunal turnover across the Ediacaran–Cambrian boundary, which is likewise reproduced by our simulations in the relatively large proportion of replicates where EEs rise to dominance (particularly where the impacts of EEs were persistent). The causes of the Ediacaran–Cambrian turnover are controversial, with alternative hypotheses favouring a dominant role of exogenous environmental change (e.g. Evans *et al.* 2022), but our results support the proposal that radical changes in the taxonomic makeup of communities can be driven by the origin of novel behaviours that change the environment, and their legacy.

CONCLUSION AND FUTURE DIRECTIONS

Our novel simulation framework provides a set of expectations for the macroevolutionary impact created by the appearance of novel behaviours in lineages that modify the fitness of other organisms (i.e. EEs). We show that the origin of EEs can be highly disruptive, introducing large variability in previously stable extinction and speciation rates in other lineages. EEs have the potential to radically alter the taxonomic makeup of ecosystems and rise to dominance. This impact is amplified by EE behaviours with a persistent impact on environments, but in all cases EE lineages are not guaranteed to dominate, and are frequently extinct by the end of the simulations. Hence we show that whilst the impacts of EEs are not deterministic, their introduction can nevertheless have profound impacts on the evolutionary trajectory and taxonomic makeup of biodiversity, having the potential to cause faunal turnovers like that seen at the Ediacaran–Cambrian transition. We must therefore consider the reciprocal impacts of changing biology on environment as we do with changing environment on biology as we piece together the history of evolving lineages through time.

With this framework, future work can focus on understanding: how engineering behaviours which do not convey maximal advantage to the engineer impact our results; whether there is predictability regarding when EE lineages do or do not take over simulations (e.g. if the disparity of populations makes them resilient to EE takeover); how the use of a spatially explicit simulation framework (e.g. REvoSim; Garwood *et al.* 2019; Furness *et al.* 2023) modifies the impact of engineers, given it is known that synergistic effects of ecosystem engineers have a measurable impact on downstream diversity in real-world settings (Gusmao *et al.* 2024); and how relaxing the assumption/property of a fixed carrying capacity modifies the impact of engineers on biodiversity.

Acknowledgements. We would like to thank the organizers of the Palaeontological Association Annual meeting in Cambridge in 2023 for convening a session on ecosystem engineering, which was the inspiration for starting this work. RJG was supported by NERC award NE/T000813/1 and the Alexander von Humboldt-Stiftung. FSD was supported by NERC fellowship NE/W00786X/1, LAP was supported by NERC fellowship NE/W007878/1. RJG and LAP were supported by Leverhulme Trust Research Project Grant 2023-234. We are grateful for thoughtful and incisive reviews by Euan N. Furness and Alison T. Cribb which significantly improved the manuscript.

Author contributions. LAP conceived the project and all authors contributed to the design of the study. RJG developed the simulation framework and added all new features to TREvoSim,

and generated data. TS performed all downstream analyses and wrote all of the R code. FSD and LAP wrote the initial draft of the manuscript with substantial input from all other authors. TS, FSD and LAP made the figures.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.9zw3r22p7.

Editor. Nicholas Butterfield

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12701):

Figures S1–S6. All results presented as speciation and extinction through time plots.

REFERENCES

Albertson, L. K., Sklar, L. S., Tumolo, B. B., Cross, W. F., Collins, S. F. and Woods, H. A. 2022. The ghosts of ecosystem engineers: legacy effects of biogenic modifications. *Functional Ecology*, **38**, 52–72.

Beekey, M. A., McCabe, D. J. and Marsden, J. E. 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. *Oecologia*, **141**, 164–170.

Butterfield, N. J. 2011. Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution*, **26**, 81–87.

Butterfield, N. J. 2017. Oxygen, animals and aquatic bioturbation: an updated account. *Geobiology*, **16**, 3–16.

Cribb, A. T., Kenchington, C. G., Koester, B., Gibson, B. M., Boag, T. H., Racicot, R. A., Mocke, H., Laflamme, M. and Darroch, S. A. F. 2019. Increase in metazoan ecosystem engineering prior to the Ediacaran–Cambrian boundary in the Nama Group, Namibia. *Royal Society Open Science*, **6**, 190548.

Darroch, S. A. F., Sperling, E. A., Boag, T. H., Racicot, R. A., Mason, S. J., Morgan, A. S., Tweedt, S., Myrow, P., Johnston, D. T., Erwin, D. H. and Laflamme, M. 2015. Biotic replacement and mass extinction of the Ediacara biota. *Proceedings of the Royal Society B*, **282**, 20151003.

Darroch, S. A., Smith, E. F., Laflamme, M. and Erwin, D. H. 2018. Ediacaran extinction and Cambrian explosion. *Trends in Ecology & Evolution*, **33**, 653–663.

Erwin, D. H. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology & Evolution*, **23**, 304–310.

Erwin, D. H. and Tweedt, S. 2012. Ecological drivers of the Ediacaran–Cambrian diversification of Metazoa. *Evolutionary Ecology*, **26**, 417–433.

Evans, S. D., Tu, C., Rizzo, A., Surprenant, R. L., Boan, P. C., McCandless, H., Marshall, N., Xiao, S. and Droser, M. L. 2022. Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition. *Proceedings of the National Academy of Sciences*, **119**, e2207475119.

Furness, E. N., Garwood, R. J. and Sutton, M. D. 2023. REvoSim v3: A fast evolutionary simulation tool with ecological processes. *Journal of Open Source Software*, **8**, 5284.

Garwood, R. J., Spencer, A. R. and Sutton, M. D. 2019. REvoSim: organism-level simulation of macro and microevolution. *Palaeontology*, **62**, 339–355.

Garwood, R. J., Spencer, A. R. T., Bates, C. T. M., Callender-Crowe, L. M., Dunn, F. S., Halliday, T. J. D., Keating, J. N., Mongiardino Koch, N., Parry, L. A., Sansom, R. S., Smith, T. J., Sutton, M. D. and Vanteghem, T. 2024. TREvoSim v3: An individual based simulation for generating trees and character data. *Journal of Open Source Software*. https://doi.org/10.21105/joss.06722

Gusmao, J. B., Rühmkorff, S., Kraufvelin, L., Meysick, L. and Pansch, C. 2024. The interplay of co-occurring ecosystem engineers shapes the structure of benthic communities – a mesocosm experiment. *Frontiers in Marine Science*, **11**, 1304442.

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S. and Wilson, W. G. 2007. Ecosystem engineering in space and time. *Ecology Letters*, **10**, 153–164.

IPBES 2023. Thematic assessment report on invasive alien species and their control. Intergovernmental Science-Policy Platform on Biodiversity & Ecosystem Services (IPBES) secretariat. https://doi.org/10.5281/zenodo.7430682

Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Keating, J. N., Sansom, R. S., Sutton, M. D., Knight, C. G. and Garwood, R. J. 2020. Morphological phylogenetics evaluated using novel evolutionary simulations. *Systematic Biology*, **69**, 897–912.

Laflamme, M., Darroch, S. A. F., Tweedt, S. M., Peterson, K. J. and Erwin, D. H. 2013. The end of the Ediacara biota: extinction, biotic replacement, or Cheshire Cat? *Gondwana Research*, **23**, 558–573.

Li, J., Ianaiev, V., Huff, A., Zalusky, J., Ozersky, T. and Katsev, S. 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. *Proceedings of the National Academy of Sciences*, **118**, e2008223118.

McMahon, W. J. and Davies, N. S. 2018. The shortage of geological evidence for pre-vegetation meandering rivers. 119–148. *In* Ghinassi, M., Colombera, L., Mountney, N. P., Reesink, A. J. H. and Bateman, M. (eds) *Fluvial meanders and their sedimentary products in the rock record*. Wiley Blackwell, 608 pp.

Mongiardino Koch, N., Garwood, R. J. and Parry, L. A. 2021. Fossils improve phylogenetic analyses of morphological characters. *Proceedings of the Royal Society B*, **288**, 20210044.

Mussini, G. and Dunn, F. S. 2023. Decline and fall of the Ediacarans: late-Neoproterozoic extinctions and the rise of the modern biosphere. *Biological Reviews*, **99**, 110–130.

Odling-Smee, F. J. 1988. Niche-constructing phenotypes. 73–132. *In* Plotkin, H. C. (ed.) *The role of behavior in evolution*. MIT Press, 208 pp.

Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**, 526–528.

R Core Team 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Reichman, O. J. and Seabloom, E. W. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution*, **17** (1), 44–49.

Ricciardi, A., Whoriskey, F. G. and Rasmussen, J. B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries & Aquatic Sciences*, **54**, 2596–2608.

Schirrmeister, B. E., Gugger, M. and Donoghue, P. C. J. 2015. Cyanobacteria and the Great Oxidation Event: evidence from genes and fossils. *Palaeontology*, **58**, 769–785.

Van de Velde, S., Mills, B. J., Meysman, F. J., Lenton, T. M. and Poulton, S. W. 2018. Early Palaeozoic ocean anoxia and global warming driven by the evolution of shallow burrowing. *Nature Communications*, **9**, 1–10.

Wilby, A. 2002. Ecosystem engineering: a trivialized concept? *Trends in Ecology & Evolution*, **17** (7), 307.

Wood, R. 1993. Nutrients, predation and the history of reef-building. *Palaios*, **8**, 526–543.

Wood, R. 2001. Biodiversity and the history of reefs. *Geological Journal*, **36**, 251–263.