Contrasting terrestrial and marine ecospace dynamics after the end-Triassic mass extinction event

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# Abstract

Mass extinctions have fundamentally altered the structure of the biosphere throughout Earth history. The ecological severity of mass extinctions is well studied in marine ecosystems by categorising marine taxa into functional groups based on ‘ecospace’ approaches, but the ecological response of terrestrial ecosystems to mass extinctions is less well understood due to the lack of a comparable methodology. Here, we present a new terrestrial ecospace framework that categorizes fauna into functional groups as defined by tiering, motility, and feeding traits. We applied the new terrestrial and traditional marine ecospace analyses to data from the Paleobiology Database across the end-Triassic mass extinction – a time of catastrophic global warming – to compare changes between the marine and terrestrial biospheres. We found that terrestrial functional groups experienced higher extinction severity, that taxonomic and functional richness are more tightly coupled in the terrestrial, and that the terrestrial realm continued to experience high ecological dissimilarity in the wake of the extinction. Although signals of extinction severity and ecological turnover are sensitive to the quality of the terrestrial fossil record, our findings suggest greater ecological pressure from the end-Triassic mass extinction on terrestrial ecosystems than marine ecosystems, contributing to more prolonged terrestrial ecological flux.

# Introduction

Mass extinction events caused by global warming and climate-related stressors throughout Earth history have profoundly impacted the ecological structure of ancient ecosystems [1–3]. In particular, previous studies focusing on marine ecospace (the combination of ecological traits that categorizes an organism’s mode of life based on shared ecological roles [4]) have noted that mass extinctions have altered the occupation of ecospace and composition of functional groups in marine ecosystems [1,3,5–7]. These studies are critical, as functional diversity is known to play a major role in modern ecosystem processes [8]. Moreover, understanding how past environmental change has affected functional diversity from the fossil record is essential for predicting the long-term ecological impacts of modern climate change. However, direct comparisons between contemporaneous changes in marine and terrestrial functional ecology from the fossil record have not previously been investigated, thus limiting our understanding of global ecological change throughout Earth history in response to ancient global warming events.

The end-Triassic mass extinction (ETE) (ca. 201.5 Ma) was the fourth of the ‘Big Five’ Phanerozoic mass extinction events [9] and profoundly impacted both marine and terrestrial ecosystems. The ETE was caused by a rapid rise in greenhouse gases due to increased volcanism from the Central Atlantic Magmatic Province (CAMP), a large igneous province associated with the rifting of the supercontinent Pangea [10,11]. The increase in greenhouse gases due to CAMP volcanism resulted in rapid global warming (~7.4°C warming at a rate greater than 10 °C/Myr [12]), causing catastrophic effects on marine and terrestrial environments and biota [13]. In marine ecosystems, ocean anoxia [14–16], ocean acidification [17,18], and decreased primary productivity [19] resulted in the total extinction of conodonts, severe losses in scleractinian corals, ammonoids, and reef-building sponges, and elevated extinction rates among articulate brachiopods, bivalves, and marine vertebrates [20–22]. Meanwhile, terrestrial ecosystems suffered from deforestation, soil loss, wildfires, and major changes in the hydrological cycle [13], resulting in significant turnovers in floral assemblages [23], increased provinciality among tetrapods [24], and heightened extinction severity among dominant tetrapod groups such as the large temnospondyl amphibian clades (e.g., the disappearance of Plagiosauridae), all but one lineage of Pseudosuchians (‘crocodile-like’ archosaurs) [25], and non-mammalian synapsids [13,26]. After the ETE, Jurassic global ecosystems were further impacted by volcanism from the Karoo-Ferrar Large Igneous Province (KFLIP) and the associated Toarcian Ocean Anoxia Event (T-OAE) [13]. Marine macroevolutionary processes continued to be driven by the ongoing Mesozoic Marine Revolution (MMR) [27,28], while terrestrial macroevolutionary processes were characterized by the diversification of dinosaurs [29]. Because marine and terrestrial ecosystems both experienced major taxonomic and ecological changes during and after the ETE, this time interval offers unique, untapped insights into comparative ecological changes in the marine and terrestrial fossil records.

Marine functional ecology in animals has been previously studied across the ETE in terms of occupation of ecospace defined by feeding, tiering, and motility [30]. Similar to previous studies of marine ecospace across the end-Permian mass extinction [5,31], on a global scale, no functional groups were lost across the ETE, and there was no significant loss in functional diversity as a result of the mass extinction [30]. However, extinction intensity was not spread evenly across all functional groups. Sessile suspension feeders and functional groups containing calcifying taxa experienced particularly high taxonomic extinction severity during the ETE [30]. Regarding terrestrial ecosystems, previous work focusing on niche partitioning in herbivorous tetrapods has identified changes in terrestrial feeding ecospace in response to environmental instability through the Triassic and Early Jurassic [32]. However, no development or application of a terrestrial ecospace using the same marine ecospace ecological traits [4] has existed to compare terrestrial and marine functional ecology. Thus, our understanding of how marine and terrestrial ecosystems comparatively change in response to the ETE, as well as other major climate change events and mass extinctions through Earth history, has been limited. Here, we present a new terrestrial ecospace framework that allows macroevolutionary and macroecological changes in marine and terrestrial ecosystems to be directly compared.

# Marine and terrestrial ecospace framework

Ecospace frameworks are one approach to defining functional groups based on shared sets of independent ecological traits that define organisms in a multi-dimensional space [33]. In previous paleoecological work, marine ecospace has commonly been defined as the combination of three ecological categories: 1) location in physical space at, above, or below the sediment-water interface (tiering), 2) potential for either motion or maintenance of a stationary position (motility), and 3) method of acquiring energy (feeding) [4,34] (Figure 1; Table S1). This defines a three-dimensional marine ecospace, where an animal’s functional group or mode of life is defined as their tiering-motility-feeding classifications [4,34]. Although more complex definitions of marine ecospace have been developed and applied [35], this simple definition has proven powerful for understanding changes in marine ecology over the course of Earth history [1,34]. Some terrestrial ecospace frameworks have been previously proposed which have reconstructed trends in terrestrial ecology through time and in the modern [36,37]. However, because selected functional traits used in the ecospace are related to the taxa and ecology being investigated, and because previous studies have not sought to directly compare changes between marine and terrestrial ecology, they lack the same equivalent marine ecospace tiering-motility-feeding ecological categories. Thus, previously developed terrestrial ecospace frameworks are limited in their utility for comparing trends in ecospace and functional ecology between the marine and terrestrial fossil records.

We present a novel terrestrial ecospace framework specifically designed to be analogous to the tiering-motility-feeding ecospace framework used for marine ecosystems [4]. Beyond incorporating the same tiering, motility, and feeding categories that define the equivalent marine ecospace, characterizing animals by these ecological traits allow us to analyse how many possible modes of life, or ecological roles, are present in a given area or given time frame [4], ultimately building a picture of how structure of marine and terrestrial ecosystems have changed over time and in response to the same climatic events. Following the equivalent marine ecospace [4], the terrestrial ecospace framework has tiering, motility, and feeding ecological categories (Figure 1; Table S2). The tiering categories are: 1) aerial, 2) arboreal, 3) ground-dwelling, 4) soil-dwelling, 5) troglobitic, and 6) aquatic. Tiering is conceptualized as the primary environment an animal is adapted for and utilizes for life history. The aerial tier applies to animals that spend significant time in the air, relying on the air for a multitude of behaviours, and are flight-adapted. Arboreal tiering applies to animals that primarily spend their time living above the ground-level in tall vegetation, like trees. Ground-dwelling tiering applies to animals that spend most of their time living and feeding on the ground. Soil-dwelling tiering applies to animals that primarily burrow into soils and live and feed underground. Troglobitic tiering refers to animals living primarily in caves. We also include an aquatic tier to include fresh-water animals, such as those living in lakes and rivers, as they are often sensitive to the environmental dynamics of terrestrial ecosystems and not included in marine ecospace analyses. The motility categories in the terrestrial ecospace are 1) migratory, 2) freely, far moving, 3) freely, short moving, 4) tethered, and 5) non-motile. Migratory animals seasonally migrate over long distances. Freely, far moving animals can move freely away from an initial habitat and over long distances (e.g., bears with large habitat ranges), whereas freely, short moving animals can also leave their initial habitats but only over relatively short distances (e.g., beavers that remain near their dams). Tethered animals are those that cannot survive if they leave their small initial habitats (e.g., icebugs that are constrained to glaciers). Non-motile animals are those which do not move at all. The feeding categories in the terrestrial ecospace are 1) predator (big), 2) predator (small), 3) omnivore, 4) herbivore, 5) scavenger, and 6) other. Predators are animals which feed on other animals as prey. Animals are classified as predator (big) or predator (small) based on the maximum size of the prey they would be likely to eat. For example, an animal classified as predator (big) can prey on megafauna or macrofauna, such as a grizzly bear preying on fish. In contrast, an animal classified as predator (small) can only prey on mesofauna, such as an insectivorous predator. Omnivores are animals which consume both plants and animals as prey. Herbivores are animals which consume plants via behaviours like browsing, foraging, and grazing. Scavengers are animals that consume dead and decaying biomass. The ‘other’ feeding category encapsulates any feeding behaviour which does not fit into the other five categories. Further details of each terrestrial ecological trait are given in Supplementary Text 1. Within this ecospace, we define a terrestrial functional group as a unique tiering-motility-feeding combination.

This terrestrial ecospace framework is a theoretical cubic ecospace designed with modern terrestrial invertebrates and vertebrates in mind. The ecological traits in each category were chosen to avoid redundancy, where a trait in one category would limit the possible traits in the other two categories to just one or two options. This maximizes the total theoretical ecospace that can be occupied by terrestrial animals. However, not every theoretical functional group of the cube is realistically occupiable. For example, an aerial, soil-dwelling, non-motile combination is an impossible mode of life, similar to how a pelagic, mining, stationary-attached category is impossible in the marine ecospace [4]. We also note that we do not expect that each viable ecological role in the terrestrial ecospace is occupied, particularly around the Triassic-Jurassic boundary, as animals have increasingly filled functional ecospace moving through Earth history towards the modern [34].

# Dataset assembly and analyses

Marine and terrestrial fossil occurrence data from the Carnian to the Aalenian (c. 237 – 174 Ma) were downloaded from the Paleobiology Database (PBDB) (accessed in June 2021). Data were processed to exclude ichnotaxa, form taxa, and uncertain taxonomic assignments. Marine and terrestrial data were initially extracted based on environment and lithology categories in the PBDB, and data were further cleaned to correct for marine and terrestrial taxa entered in the paleoenvironments in which they were preserved rather than lived (e.g., terrestrial vertebrates preserved in marine sediments due to bloat-and-float). Marine taxa belong to the phyla Annelida, Arthropoda, Brachiopoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Hemichordata, Mollusca, Nematoda, and Porifera. Terrestrial taxa belong to the phyla Arthropoda, Chordata, and Mollusca. The protocols taxonomic and environmental filtering and stratigraphic binning to give each occurrence a stage assignment follow ref. [38]. Ecospace assignments for tiering, motility, and feeding were made at the genus level. Ecospace assignments were based on a combination of previous ecospace literature [5,30], functional morphology, ecological information of extant relatives, and according to the ecology categories information given in the PBDB. Genera were removed from the dataset when a functional group assignment could not be made due to insufficient information. This resulted in 86 terrestrial insect taxa and 19 marine genera being removed from the final datasets. After data cleaning and removal of taxa without functional group assignments, the dataset contains 56,173 marine fossil occurrences with 2481 unique genera, and 2028 terrestrial fossil occurrences with 630 unique genera.

To assess the impact of the ETE on functional ecology, we conducted analyses on functional and taxonomic diversity, extinction dynamics within functional groups, and ecological dissimilarity during the ETE and the Early Jurassic. Our analyses largely follow previous marine ecospace work [5,30] in order to make cross-study comparisons. Functional and taxonomic diversity were determined by calculating functional group and generic richness (the number of unique functional groups or genera in each stage, respectively). For within-functional group dynamics, we calculated the relative abundance of functional groups in each stage in terms of PBDB fossil occurrences and generic richness, as well as the extinction severity of each functional group. Extinction severity was determined by calculating the percentage of pre-ETE (Rhaetian) genera that do not reappear in the Early Jurassic. Finally, to assess ecological stability, we calculated Bray-Curtis dissimilarity indices [39] comparing the functional group composition between preceding stages (e.g., Norian and Carnian, Pliensbachian and Sinemurian) and between each Jurassic stage and the Rhaetian [30]. To account for sampling biases in the marine and terrestrial fossil records, we applied a collection-level bootstrap subsampling protocol, with subsampling quotas set at *n*=400 collections for marine analyses (average 3.7 occurrences per collection) and *n*=35 collections for terrestrial analyses (average of 3.0 occurrences per collection). For the terrestrial analyses, the Carnian and Aalenian were excluded from subsampling due to very low sample size. For each analysis, the subsampling protocol was applied for 1000 iterations to obtain a distribution of results with a final mean value and 95% confidence intervals.

# Results

## *Occupation of marine and terrestrial ecospace*

In the marine realm, 39 ecospace functional groups were present from the Carnian through the Aalenian. The majority of functional groups present were in the surficial, semi-infaunal, and shallow infaunal tiers, although the highest occupied functional group was the pelagic, freely fast-moving predators (FG 115) (Figure 1A). This group includes animals like cartilaginous fishes, secondarily aquatic tetrapods, and ammonites. Epifaunal attached stationary suspension feeders (FG 361) were the second most occupied functional group, occupied by fauna such as demosponges and brachiopods, followed by surficial freely slow-moving grazers (FG 324), which are largely represented by gastropods and ostracods. In the terrestrial realm, 33 ecospace functional groups were present, with most occupied functional groups in the ground-dwelling and aquatic tiers (Figure 1B). Ground-dwelling freely far-moving herbivores (FG 324), represented by dicynodonts and early dinosaurs, and aquatic freely short-moving large predators (FG 631), like non-marine hybodont sharks, were the most common terrestrial functional groups. We identified no taxa as cave-dwelling animals from the Carnian to the Aalenian, so the troglobitic ecospace tier is unoccupied.

## *Taxonomic and functional richness*

In the marine, 70.6% (± 4.82%) of Rhaetian genera went extinct between the Rhaetian and Hettangian, a similar result to previous estimates [30]. The Rhaetian-Hettangian boundary was the significantly highest interval of extinction severity for this time interval (Supplementary Figure 1). Marine generic richness was highest prior to the extinction interval in the Norian, followed by a significant decline through the Rhaetian and into the Hettangian. Marine generic richness then increased gradually in the Jurassic until a slight decline between the Pliensbachian and the Toarcian (Figure 2A). In contrast, marine functional richness increased through the Late Triassic, reaching its acme in the Rhaetian, followed by a marginal decline across the mass extinction interval into the Hettangian. Marine functional richness was then relatively stable until a slight peak in the Pliensbachian, followed by a gradual decline into the Toarcian and Aalenian (Figure 2A). In contrast, terrestrial extinction severity was significantly higher. Across the Rhaetian-Hettangian boundary, 95.9% (± 3.93%) of terrestrial genera go extinct, which is the highest terrestrial extinction severity for this time interval (Supplementary Figure 1). Terrestrial generic richness was relatively stable between the Norian and Rhaetian, followed by a significant decline into the Hettangian. Terrestrial generic richness then continued to increase through the Early Jurassic, until reaching its peak in the Toarcian (Figure 2B). Terrestrial functional richness followed a similar pattern, with unchanging functional richness between the Norian and the Rhaetian followed by a decline in the Hettangian, and then continuously increasing until the Pliensbachian (Figure 2B).

## *Within-functional group dynamics*

The patterns in functional group occurrences and generic richness changed in both the marine and the terrestrial records. In the marine, pelagic freely fast-moving predators (FG 115) and epifaunal attached stationary suspension feeders (FG 361) were consistently the two functional groups occupied by the most genera. However, which of the two groups was the dominant (i.e., most taxonomically occupied) functional group changed across the extinction interval (Figure 3A). In the Norian and Rhaetian, epifaunal attached stationary suspension feeders were the dominant functional group, comprising about 36% of all marine genera occurrences. From the Hettangian to the Toarcian, the pelagic freely fast-moving predators were the dominant functional groups, representing 36% to 47% of all Early Jurassic marine genera. The third most dominant marine functional group was the erect attached stationary suspension feeders (FG 261), which represented about 13% of all marine genera occurrences in the Norian and Rhaetian and then declined to only around 3% of marine genera beginning in the Hettangian and through to the Toarcian. In their place, epifaunal freely slow-moving grazers (FG 324) became the third most occupied functional group beginning in the Hettangian. In terms of marine generic richness, we found the same general patterns as with marine generic occurrences, although the magnitude of the changes is lower (Figure 3B). Marine generic richness is more evenly distributed among the functional groups, particularly after the extinction interval. For example, pelagic freely fast-moving predators and epifaunal attached stationary suspension feeders were still the functional groups with the most unique genera, but they only represented a combined approximately 45% of the unique genera present beginning in the Hettangian and continuing through the Early Jurassic. Less well occupied functional groups such as epifaunal freely slow-moving grazers (FG 324), shallow-infaunal attached stationary suspension feeders (FG 461), and deep-infaunal unattached facultatively mobile suspension feeders (FG 631) were better represented in terms of generic richness. Erect attached stationary suspension feeders (FG 261) were also impacted in terms of generic richness, but less severely than in terms of occurrences (Figure 3B).

Patterns in terrestrial functional groups are even more dynamic for both occurrences and generic richness (Figure 4). The most significant change in terrestrial functional group occurrences is in the aquatic tier, in which aquatic freely short-moving large predators (FG 631) comprised of approximately 25% of all terrestrial generic occurrences in the Norian and Rhaetian but collapsed significantly to less than 5% of generic occurrences after the mass extinction interval (Figure 4A). The same pattern and magnitude are true for the aquatic-tier functional groups when considering generic richness within terrestrial functional groups (Figure 4B). Outside of the aquatic tier, terrestrial functional group dominance changed dynamically between stages. For example, in the Norian, ground dwelling freely far-moving herbivores (FG 324) were the most dominant group, but it quickly collapsed, and ground-dwelling and arboreal freely short-moving small predators (FG 232 and FG 332, respectively) became the dominant functional groups in the Rhaetian (Figure 4A). Through the mass extinction interval and into the Hettangian, the ground-dwelling freely far-moving herbivores regained dominance, representing over a third of all terrestrial genera occurrences. Concurrently, there was a significant expansion within the ground-dwelling tier. Over three-quarters of all terrestrial genera occurrences in the Hettangian belonged to ground-dwelling functional groups (Figure 4A). Occurrences of arboreal-tier functional groups increased through the Jurassic, particularly driven by the rise of arboreal freely short-moving herbivores (FG 234) beginning in the Sinemurian, which is the most occupied arboreal functional group by the Toarcian (Figure 4A). Aerial-tier functional groups, which were barely represented in the Triassic, also represent an increasing proportion of terrestrial genera occurrences in the Jurassic (Figure 4A). By the Toarcian, aerial freely short-moving small predators (FG 132) (e.g., crown group dragonflies) and herbivores (FG 134) represented over 40% of all terrestrial genera occurrences. When accounting for the relative abundance of terrestrial functional groups in terms of generic richness, we find the same patterns occur at very similar magnitudes (Figure 4B). The only major difference between the results based on occurrences versus functional richness is in the ground-dwelling freely short-moving large predator functional group (FG 321), which increased in the total number of generic occurrences in the functional group from the Rhaetian to the Hettangian, but not in terms of the generic richness of the functional group (Figure 4).

## *Within-functional group extinction severity*

There were 33 marine functional groups present in the Rhaetian, which all experienced some level of extinction. The least impacted functional groups were the deep-infaunal unattached facultatively mobile deposit feeders (FG 632) and the shallow-infaunal attached facultatively mobile ‘other’ feeders (FG 546). For both groups, less than 1% of the Rhaetian genera disappeared in the Early Jurassic. Within 22 marine functional groups, at least half of the Rhaetian genera went extinct in the Hettangian and did not reappear by the Aalenian, and 8 functional groups experienced 100% extinction of all the Rhaetian genera (Figure 5A). However, most of the functional groups that lost all of their Rhaetian genera had enough taxonomic turnover that they did not disappear (Supplementary Figures 2-3). For example, within the erect facultatively attached suspension feeders group (FG 241), only two crinoid genera from the Paracomatuliae and Tulipacrinidae families occupied the group in the Rhaetian, which are replaced by crinoids in the Pentacrinitidae family in the Hettangian and Sinemurian, and then replaced by stalked benthic crinoids from the Isocrinida family by the Toarcian. Only the semi-infaunal unattached stationary ‘other’ feeders (FG 456) and the shallow-infaunal freely slow-moving predators (FG 521) disappeared in the Hettangian and did not reappear by the Aalenian, driven by the extinction of various bivalve taxa.

Terrestrial functional groups experienced higher extinction severity compared to the marine functional groups. There were 24 terrestrial functional groups in the Rhaetian. In all 24 functional groups, at least half of the pre-extinction genera disappeared between the Rhaetian and Hettangian and did not reappear by the Aalenian. Seventeen functional groups lost 100% of the genera that were present in the Rhaetian (Figure 5B). However, much like the marine functional groups with very high extinction severity, not all those 17 functional groups disappeared, as there was sufficient turnover for the majority of the terrestrial function groups to persist (Supplementary Figure 2). For example, in the arboreal, freely short-moving small predators group (FG 232), the mammaliaform haramiyidans and lizard-like kuehneosaurids were replaced by other small mammaliaform insectivores, including triconodontids and cotylosaurs, in the Hettangian and Sinemurian, while morganucodonts persisted in the group across the extinction interval. Only three terrestrial functional groups disappeared entirely between the Hettangian and Aalenian: arboreal freely short-moving ‘other’ feeders (FG 236), ground-dwelling freely far-moving omnivores (FG 323), and aquatic freely far-moving large predators (FG 621). Their disappearances were driven by the extinction among Triassic reptiles, including drepanosaurs and parasuchid phytosaurs.

## *Ecological dissimilarity through time*

Bray-Curtis dissimilarity indices indicate differences in ecological similarity and stability through time between the marine and terrestrial fossil records (Figure 6). When comparing the ecological structures of consecutive marine stages, the highest dissimilarity is observed between the Rhaetian and the Hettangian, just after the mass extinction interval. Dissimilarity then decreased through the Jurassic to its lowest point between the Sinemurian and the Pliensbachian, and slightly increased again to the Toarcian and Aalenian (Figure 6A). In the terrestrial, the greatest dissimilarity between preceding stages also occurred in between the Rhaetian and the Hettangian, just after the mass extinction interval. Dissimilarity then decreased between the Hettangian and Sinemurian but increased again through the Pliensbachian and Toarcian (Figure 6B). Overall, dissimilarity between consecutive terrestrial stages was significantly higher than dissimilarity between consecutive marine stages (Figure 6).

The marine and terrestrial records also differ when comparing ecological composition of the Jurassic stages to the Rhaetian. In the marine, all the Jurassic stages were more dissimilar to the Rhaetian than they are to each other. Ecological dissimilarity to the Rhaetian decreased only slightly through time in the Pliensbachian but then increased again in the Toarcian and Aalenian (Figure 6A). In general, however, all the marine stages were relatively equally dissimilar to the Rhaetian, as the Jurassic Bray-Curtis indices broadly average around 0.30 (Figure 6A). In comparison, the Bray-Curtis indices comparing terrestrial Jurassic stages to the Rhaetian in the terrestrial are, again, much higher than they are in the marine (Figure 6B). Additionally, the ecological dissimilarity increased through the Early Jurassic (Figure 6B).

# Discussion

When comparing marine and terrestrial ecospace dynamics across the end-Triassic mass extinction event, three key differences emerge. First, taxonomic and functional richness were more tightly coupled in the terrestrial fossil record than they were in the marine fossil record across the ETE. Second, extinction severity within terrestrial functional groups was much higher than within marine functional groups. Third, terrestrial ecosystems sustained high ecological dissimilarity through the wake of the ETE, suggesting protracted ecological flux in the terrestrial realm through the Early Jurassic.

Terrestrial functional group richness and taxonomic richness are coupled, both decreasing across the extinction interval (Figure 2). This stands in contrast to marine taxonomic and ecological decoupling, where functional group richness does not decline as severely as taxonomic richness (Figure 2A). Coupling in the terrestrial realm also contrasts other mass extinction intervals [5,30,40,41]. Coupling between taxonomic and functional group richness in the terrestrial realm through the ETE is due to a lack of redundancy both within each functional group (referring to the low number of taxa that occur in each functional group (Figure 1B)) and within genera (referring to the high number of genera that are represented by five or fewer occurrences in each stage (Supplementary Figure 4)). Terrestrial functional group richness was sensitive to taxonomic losses because the functional groups were only occupied by a few genera represented by only a small number of fossil occurrences, and thus were relatively unbuffered to taxonomic extinction severity. While this is certainly influenced by poor quality of the terrestrial fossil record for this time interval, it may also be a true signal of continued terrestrial ecosystem stress, as the ETE and prolonged environmental instability [42] may have also driven mass rarity [43] leading to a higher proportion of genera with very low abundances in the Early Jurassic (Supplementary Figure 4). Taxonomic and ecological decoupling during mass extinction intervals is important for the persistence of ecosystem stability. Maintaining high functional diversity may keep ecosystems from ecological collapse, particularly if the surviving functional groups represent ecologically important groups such as keystone species [41]. Thus, the lack of taxonomic redundancy within terrestrial functional groups may have ultimately resulted in terrestrial ecosystems that were particularly sensitive to ecological collapse. While these patterns may be primarily a signal of the quality of the terrestrial fossil record, these results still demonstrate how depauperate functional groups are still extremely sensitive to extinction.

The differences in marine and terrestrial ecological dissimilarity after the ETE suggest that terrestrial ecosystems were in a more prolonged state of ecological instability. For both the marine and terrestrial records, the highest sequential ecological dissimilarity occurred between the Rhaetian and the Hettangian (Figure 6). This is unsurprising, given that ecosystems are expected to be in a state of ecological transition or flux just after mass extinction events [43,44]. While the marine realm gradually returned to low ecological dissimilarity in the wake of the ETE, terrestrial ecological dissimilarity between sequential stages remained high (Figure 6). These results imply marine ecosystems were becoming more ecologically stable by the Sinemurian and Pliensbachian, while terrestrial ecosystems were continuing to experience pressure and ecological flux due to prolonged impacts of the ETE [43,44]. Even beyond the ETE, continued volcanic activity associated with the rifting of Pangea through the Middle Jurassic caused terrestrial carbon cycle perturbations and floral turnover [42], which may have contributed to prolonged terrestrial ecological instability, particularly in the Toarcian and Aalenian. Terrestrial ecological dissimilarity between stages was also always higher than marine dissimilarity (Figure 6). This elevated terrestrial ecological dissimilarity was driven by high extinction severity within most functional groups (Figure 5) followed by the turnover to new genera in different functional groups between stages (Supplementary Figure 2). Ultimately, these processes result in the very dynamic changes in functional group composition of each stage observed throughout this entire time interval (Figure 4).

Moreover, when comparing the ecological dissimilarity of each Jurassic stage to the Rhaetian, terrestrial ecosystems appear to have been evolving into a very different ecological realm. Ecological dissimilarity between Jurassic stages and the Rhaetian for terrestrial ecosystems continued to increase through each Jurassic stage (Figure 6B). This implies that terrestrial ecosystems were in such high flux that they were evolving into a new, post-extinction ecological state, apparently largely driven by expansions in ground dwelling- and aerial-tier functional groups and the near total collapse of the aquatic tier in the Jurassic (Figure 4). Meanwhile, marine ecological dissimilarity between the Jurassic stages and the Rhaetian are much lower than in the terrestrial realm, and the level of dissimilarity is relatively stable from the Hettangian through the Aalenian (Figure 6). Because genus longevity is not substantially different between the marine and terrestrial fossil records for this time interval (Supplementary Figure 5), the greater stability in marine ecosystems is likely due to new genera emerging with similar ecological traits as those that went extinct. Meanwhile, instability in terrestrial ecosystems is likely attributed to new genera emerging with different ecological traits (Supplementary Figure 2). This most likely reflects emerging ecologies responding to profoundly changing terrestrial landscapes in the Jurassic due to changing flora [23]. Another contributing factor may be that the terrestrial ecospace is generally more open and less occupied (Figure 1), such that more ecospace functional groups are available for emerging terrestrial groups to radiate into throughout the Jurassic.

In general, our results for both marine and terrestrial ecospace changes are aligned with several conclusions from previous research that utilize different methodologies. First, the results presented here are consistent with previous marine ecospace research across the ETE, even while using slightly different datasets and subsampling protocols (Supplementary Figure 6) [30]. Second, the survival of most functional groups despite high extinction severity in both the marine and terrestrial realms aligns with previous research which demonstrated that functional groups are difficult to lose as long as they are occupied by a few resilient taxa [5]. Third, terrestrial ecological flux being driven by ground-dwelling and aerial-tier functional groups is consistent with the previously observed broad-scale faunal turnover in Early Jurassic ecosystems that was driven by the rise of large herbivorous dinosaurs [45] and pterosaurs [46], and likely reflects changes in terrestrial landscapes associated with the ETE [13,23]. Finally, previous research has focused on turnover among insects through this time interval, and although it is unclear from our results whether the ETE significantly affected insect diversification and extinction rates [41,47], the changes exhibited in ecospace occupation in major insect groups (e.g., cockroaches, omnivorous beetles) suggest that major disruptions to ecosystem structure substantially affected insect ecological partitioning. Thus, our results largely align with previous observations and interpretations of broader terrestrial faunal dynamics across the ETE, and support previous hypotheses that the ETE was more severe for the terrestrial realm than for the marine realm [41].

There are several biases in the fossil record that may influence these results. First, the terrestrial fossil record passes through more significant taphonomic filters than the marine fossil record does. Sediments deposited in fluvial and lacustrine systems preserve the bulk of our sampled vertebrate fossils (Supplementary Figure 7). The constant cycling between erosion, transport, and deposition in these systems significantly decreases the preservation potential of any organism, but especially for animals that preserve disarticulated parts (e.g., vertebrates, arthropods). There are also taphonomic biases within the terrestrial cube itself. For example, while the terrestrial aquatic tier is particularly sensitive to global warming in terms of physiological stress on animals, it is also sensitive to global warming with respect to the preservation of the tier itself as lakes dry up in response to warming climates. This may drive some of the results in terms of the collapse of the aquatic tier. Additionally, the fidelity of marine ecospace assignments is sensitive to preservation quality which, for example, would have changed in response to ocean acidification as fossils of calcifying taxa lose detail needed for detailed taxonomic assignments due to dissolution. Moreover, functional groups that may tend to be occupied by nektonic or soft-bodied organisms will have lower occupancy due to their lower preservation potential. Finally, although we have corrected for sampling biases in both the marine and terrestrial fossil records, rarefaction curves for each stage indicate that low numbers of fossils in most of the terrestrial fossil record, and also during the Carnian for the marine record, may impact some of the results observed here (Supplementary Figures 8-9).

There are also unique taxonomic biases in the terrestrial fossil record. Specifically, many ecospace assignments were hampered by outdated taxonomic assessments in the terrestrial fossil record, which was a taxonomically wide-reaching problem that is present in most, if not all, of the terrestrial ecospace functional groups. Additionally, because terrestrial fauna during this time period are often represented by disarticulated fossils, the limited availability of anatomical information creates some degree of taxonomic and ecological uncertainty. For example, insect ecospace assignments were often made based on taxonomic relationships and inferred similarity to modern insects, although we note that future work utilizing recent advances in dietary inferences in small, extinct taxa [48] would decrease this particular bias. Finally, when assessing extinction severity across the ETE, it is also important to consider that the terrestrial fossil record is dominated by monospecific genera, where low within-genus redundancy in the fossil record is also a result of only one species being assigned to the genus, and this may lead to artificially inflated levels of extinction. However, comparing the patchy terrestrial record and less-patchy marine record (Supplementary Figure 4) shows that even with higher percentages of singleton genera and elevated rates of generic turnover across geologic stage, we still observe similar extinction patterns in both the marine and terrestrial records. Overall, we emphasize that it is important to consider these biases when interpreting broad-scale patterns in the record of terrestrial ecological change through time. However, given the decoupling between singleton dominance and extinction severity (Supplementary Figure 4) as well as the context of our results within previously described terrestrial ecosystem restructuring, we conclude that our results are still reflect a genuine ecological signal across the ETE.

The results of the new terrestrial ecospace framework presented here are promising in terms of building avenues for future work. First, Early Jurassic terrestrial ecosystems appear to have experienced considerably high and prolonged ecological instability, precise drivers have not been identified. It is possible some very ecologically important terrestrial taxa such as keystone species or ecosystem engineers may have been disproportionately impacted by the ETE and ultimately resulted in disruptions to key terrestrial Earth systems processes that contributed to persistent ecological disequilibrium [44]. Additionally, the terrestrial ecospace framework needs to be applied to other time intervals. It remains unclear whether the trends of ecological instability in the terrestrial realm are unique to the ETE, a recurring pattern during other mass extinction events and periods of major global environmental perturbations, or a general characteristic of the terrestrial fossil record. Therefore, applying this new terrestrial ecospace framework to other time periods throughout Earth history will be important for contextualizing these results.

Finally, we note that there are expansions that could be made to the general ecospace framework. While the coarse resolution of a three-category ecological trait framework is beneficial in it can be applied to a taxonomically diverse set of fossil taxa, it may overlook important finer-resolution ecological change. Limitations of this coarse marine ecospace have been previously discussed [4]. This terrestrial ecospace framework does not distinguish important changes that may occur within coarse ecospace traits. For example, the signal for the significant ecological shifts within terrestrial herbivores in the Triassic [32] would not be captured by terrestrial ecospace at this resolution. Additionally, previous analyses of higher-dimensional ecospace have been able to answer questions relating to biotic interactions within functional groups, physiological stress, and habitat change [49–52] by incorporating additional relevant ecological traits. Similarly, due to the lack of physiology-related traits, such as body size and respiration types, this ecospace is not entirely appropriate to assess extinction selectivity during time intervals of severe climate-related stress. Therefore, we emphasize that this definition of terrestrial and marine ecospace should only be used for appropriate questions regarding macroevolutionary and macroecological trends in and between the marine and terrestrial records (see similar discussions in ref. [4]). However, the simplicity of the terrestrial ecospace framework presented here remains powerful in that it is directly comparable to a previously existing and widely used marine ecospace framework, and in that both ecospace frameworks utilize data that is readily available in open-source community databases, such as the Paleobiology Database.

**Conclusions**

The development of a terrestrial ecospace framework to reconstruct trends in functional ecology comparative to marine trends has illuminated new insights in how terrestrial ecosystems responded to the ETE, a time of catastrophic rise in greenhouse gases. A lack of functional redundancy in the terrestrial realm likely drove taxonomic-ecological coupling in terms of extinction severity, which is not observed in the marine. Terrestrial functional groups also experienced much higher extinction severity than marine functional groups did, which was driven by a lack of redundancy within functional groups, as well as the high number of terrestrial genera with very low abundances in the fossil record. Finally, our results overall indicate continuous functional group turnover and ecological flux in terrestrial ecosystems through the Jurassic, contrasting with the earliest establishment of ecological stability in the marine. Important future work should constrain whether these differences between the marine and terrestrial records are unique to the ETE, consistent across extinction events, or a general characteristic of terrestrial ecosystems. However, we do emphasize that these signals of prolonged terrestrial ecological flux are also sensitive to the quality of the Early Triassic fossil record. Poor preservation of terrestrial biodiversity leads to a small number of fossil occurrences and only a few representative taxa for each genus in each stage. This can artificially inflate how sensitive each terrestrial clade and functional group are to extinction and turnover, as it is easier to lose groups from the fossil record if they already appear depauperate due to taphonomic filters. Important avenues of future work will involve testing the sensitivity of the ecological signals described here to the quality of the fossil record. Even still, these results demonstrate the unique utility of the novel terrestrial ecospace framework presented here, underscore the severity of the ETE for ecosystems beyond the marine biosphere, and suggest that the extinction event was most ecologically severe for terrestrial ecosystems. In general, these results may be important for understanding how terrestrial and marine ecosystems will respond to rapid anthropogenic climate change on geologic and evolutionary timescales.

# Figures



**Figure 1: Ecospace cubes and taxonomic occupation.** Marine (A) and terrestrial (B) ecospace cubes with functional groups colour coded for occupation. Filled in cubes represent functional groups that are present at least once in the Carnian to Aalenian dataset. Functional groups represented by dark purple cubes are sparsely occupied, whereas functional groups represented by light yellow groups are abundantly occupied. Colour scale corresponds to the log number of genera occupying each functional group



**Figure 2: Generic and functional group richness.** Taxonomic (generic) and functional richness for the marine (a) and terrestrial (b) fossil records. Generic richness curves are plotted in purple and functional richness curves are plotted in orange. Error bars are 95% confidence intervals calculated from bootstrap subsampling. Carnian and Aalenian data is missing for the terrestrial due to insufficient raw Paleobiology Database (PBDB) data size for subsampling. Stage abbreviations are Cr=Carnian, Nrn=Norian, Rht=Rhaetian, Htt=Hettangian, Snm=Sinemurian, Pl=Pliensbachian, Trc=Toarcian, and Aln=Alenian.

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**Figure 3: Relative abundance of marine functional groups.** Relative abundance of marine functional groups calculated from total taxonomic occurrences (A) and from unique genera (B). Colors are divided into the ecospace tier, and shades within each color are different feeding-motility functional group combinations. Stage abbreviations consistent with previous figures.



**Figure 4: Relative abundance of terrestrial functional groups.** Relative abundance of terrestrial functional groups calculated from total taxonomic occurrences (A) and from unique genera (B). Colors are divided into the ecospace tier, and shades within each color are different feeding-motility functional group combinations. Data is not presented for the Carnian or Aalenian due to their PBDB sample sizes being too small to subsample. Stage abbreviations consistent with previous figures.



**Figure 5: Within-functional group extinction severity.** Generic extinction severity of marine functional groups (A) and terrestrial functional groups (B). Extinction severity is calculated as the percentage of genera in the Rhaetian that are not present in the Jurassic from the Hettangian to the Aalenian. Error bars are 95% confidence intervals from bootstrap subsampling.



**Figure 6: Bray-Curtis dissimilarity indices through the ETE.** Ecological dissimilarity of functional group composition between stages for the marine (A) and terrestrial (B) fossil records. Ecological dissimilarity calculated as Bray-Curtis dissimilarity indices, where 1 is most dissimilar and 0 is the same functional group composition. Star-dash lines are comparing each Jurassic stage to the Rhaetian, and circle-dash lines are comparing each stage to its preceding stage. Error bars are 95% confidence intervals calculated from bootstrap subsampling. Red dashed line represents the extinction event. Stage abbreviations consistent with previous figures.

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**Data accessibility statement**

Terrestrial and marine datasets have been uploaded as part of the electronic supplementary information. These datasets as well as all R code written to conduct these analyses are freely availability on Zenodo (doi: 10.5281/zenodo.8398420) and in this project’s GitHub repository (https://github.com/atcribb/Terrestrial-and-marine-ecospace-through-the-ETE).

**Author contribution statement**

A.T.C. and K.K.F. conceptualized the research and designed the research plan with input from F.A.C. and D.J.B. A.T.C, J.B, S.K.B, V.C.C, and P.M. made marine ecospace assignments. A.T.C., K.K.F., C.H.W., J.B., and C.H.W. made terrestrial ecospace assignments. A.T.C. performed all statistical analyses. A.T.C., K.K.F., and C.H.W. wrote the manuscript with input from all co-authors.

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