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# Life on a tropical planet: niche conservatism and the global diversity gradient

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## ABSTRACT

**Aim** The niche conservatism hypothesis proposes that species distribution patterns are, by and large, governed by ancestral climatic affinities. Here, we test this hypothesis by combining information on current diversity gradients among lineages, lineage initiation dates, and palaeoclimatic reconstructions.

**Location** World-wide.

**Methods** We test the niche conservatism hypothesis by comparing slopes of latitudinal diversity gradients among terrestrial and aquatic lineages derived from 343 studies from around the world. The prediction is that clades originating during warm periods should be very species rich in tropical regions, exhibiting a steeper richness gradient from lower to higher latitudes than clades originating during cold periods, which are expected to exhibit shallower latitudinal species richness gradients.

**Results** Latitudinal gradients for clades that originated in warm climates are steeper and with a strong tropical affinity, whereas organisms originating in colder periods exhibit a shallower diversity gradient or no tropical affinity.

**Conclusions** For a broad variety of plants and animals of both marine and terrestrial realms our results are consistent with the idea that higher diversities have arisen among tropical clades because the earth has been predominantly tropical throughout most of its history. Most clades radiated in tropical climates, with subsequent climate changes causing a retraction in distributions. Our study implies that global climate change by itself, even when developing over tens of millions of years, could have shaped the large-scale patterns of diversity prevailing on earth today.

## Keywords

Clade radiation patterns, fossil record, latitudinal diversity gradient, macroecology, niche Conservatism, palaeoclimate.

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## INTRODUCTION

Despite two centuries of research, the extraordinarily high biological diversity of tropical regions continues to galvanize scientific debate (Hawkins *et al.*, 2003; Willig *et al.*, 2003). Although correlating with current climate patterns, the peak in diversity remains unexplained from a theoretical and evolutionary perspective (see for discussion Currie *et al.*, 2004; Jablonski *et al.*, 2006; Jablonski, 2007; Mittelbach *et al.*, 2007). The niche conservatism hypothesis proposes that species distribu-

tion patterns are, by and large, governed by ancestral climatic affinities. Explicit hypotheses pertaining to current climate have so far failed to provide unequivocal mechanisms explaining the latitudinal diversity gradient, underlining the importance of studying evolutionary influences on the formation of diversity patterns (e.g. Jablonski, 2007; Mittelbach *et al.*, 2007). One factor that might affect the distribution of species is outlined by the species niche conservatism hypothesis, i.e. the concept that organisms retain their ancestral ecological preferences over time and space (e.g. Wiens & Graham, 2005; Wiens

*et al.*, 2010; see also Losos, 2008). The tropical niche conservatism hypothesis proposes that most clades have tropical origins and, since niches are conserved, the colonization of non-tropical regions by these clades is slow (Wiens & Donoghue, 2004) and has furthermore been cyclically perturbed by glacial–interglacial periods at high latitudes. This hypothesis implies that historical climate has determined the sizes of pools available for the occupancy of earth’s major bioclimatic regions (i.e. tropical, subtropical, temperate and polar regions), whereas current climate constrains the species distributions of these clades (Wiens, 2004; Wiens & Donoghue, 2004; Fine & Ree, 2006; Araújo *et al.*, 2008). Other evolutionary mechanisms have been proposed to explain the extraordinary diversity of the tropics. They include those encompassing an increased level of steady-state equilibrium of speciation–extinction as a function of area (Rosenzweig, 1992), the greater age of the tropics (Pianka, 1966), as well as intrinsic differences in diversification rates between the tropics and non-tropical regions (Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007; Weir & Schluter, 2007; Wiens, 2007).

In this paper, we test if a prediction derived from the tropical niche conservatism hypothesis is met by analysing the slope of latitudinal diversity gradients derived from 343 studies from around the world. These studies represent a wide-ranging sampling of diverse taxonomic groups from across the ‘tree of life’, representing both terrestrial and aquatic lineages. If niche conservatism is involved in shaping the current distribution of diversity of life, clades originating during warm periods would be very species rich in tropical regions, exhibiting a steeper diversity gradient from lower to higher latitudes than clades originating during cold periods, which would be expected to exhibit a shallower latitudinal diversity gradient. To test this prediction, we constructed a timeline of global climatic variation for the past 750 million years. Estimates of variation in global temperatures were adopted as an approximate correlate of the geographical extent of climatic zones (Ruddiman, 2001). We distinguished between five palaeoclimatic categories and clades were grouped by the palaeoclimatic category in which they are expected to have originated. Because information about the particular places and environments where clades originated is missing, an assumption was made that the probability of a clade originating in a given climate is, all else being equal, correlated with the palaeoclimatic category in which they are expected to have originated. The results are consistent with the idea that current diversity gradients carry the footprint of historical climates, and invite the interpretation that niche conservatism is at least one of the mechanisms involved in generating the current diversity gradient.

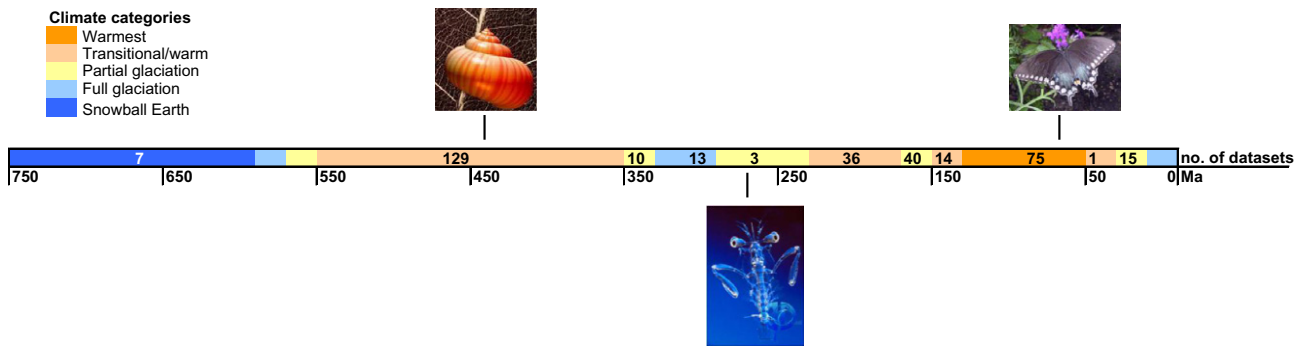
## METHODS

Data on the shape of the present-day latitudinal diversity gradients of clades were compiled from the meta-analysis study of latitudinal gradients by Hillebrand (2004) (Table S1 in Supporting Information). Periods of clade initiations were estimated from the fossil record (Benton, 1990; Benton, 1993; Nielsen,

2001). The slope  $b$  of the regression coefficient of latitude against richness was determined, thereby characterizing the strength of the richness gradient for each clade. Only datasets associated with latitudinal gradients larger than 30° were included in the analysis. Obvious polyphyletic groups, such as marine and herbivorous mammals, were excluded from the dataset, as the age of monophyletic groups was our variable of interest. We also excluded data from studies on miscellaneous parasites and non-taxonomically defined groups such as the zoobenthos. Clade level ranged from genus to phylum, and the time of initiation varied accordingly, from 16 to 630 million years ago (Ma) (Hillebrand, 2004).

As estimation of climate in deep geological time is difficult and associated with noticeable errors of measurement (Ruddiman, 2001), we only distinguished between five broad palaeoclimatic categories: (1) ‘snowball earth’, representing the coldest stage; (2) full glaciation; (3) partial glaciation; (4) transitional/warm; and (5) warm (Fig. 1, Table 1). Clades were grouped by the palaeoclimatic category in which they originated, under the assumption that the probability of a clade originating in a given climate type is, all else being equal, correlated with palaeoclimatic category (i.e. a high global temperature would indicate probable tropical origin). This is, of course, a simplifying assumption that may cause noise in the analysis, but general patterns might still emerge from it. Evidence of Palaeozoic and Mesozoic climate variation is mainly derived from continental sedimentary deposits, which may be dated by measuring the radioactive decay of specific, unstable isotopes, while evidence for more recent climatic variation can be obtained from either oceanic and lake sediment deposits or biotic and geochemical proxies (Ruddiman, 2001). At present, there is broad consensus on dating the most major trends within the climatic history of the earth (Table 1). Between 850 and 550 Ma, earth was at its coldest known state, and complex organisms only evolved after this period. Subsequently, it is believed only two major periods of glaciation occurred, the first between 325 and 240 Ma, and the second being the present cool period (see Table 1). An additional glaciation occurred at about 430 Ma, but it is now considered to have been very brief (Ruddiman, 2001). Earth was essentially a tropical planet during the Cambrian ‘explosion’, when most phyla originated, as well as during the Mesozoic and early Tertiary periods, when most modern organisms evolved. During periods of glaciation, such as the current cool period, the tropical belt is diminished, while the latitudinal temperature gradient steepens (Dimichele *et al.*, 2001).

Due to the significant variation in the number of studies available for each palaeoclimatic category, the average latitudinal gradients of diversity for clades initiated in different categories were compared using the nonparametric Kruskal–Wallis one-way analysis of variance by ranks. Subsequently, latitudinal gradients of diversity were compared between specific pairs of climatic categories using the Wilcoxon signed-rank test. In order to facilitate the presentation of results, slope values were reversed, resulting in a greater positive slope correlating with greater tropical affinity.



**Figure 1** Basic timeline of the study. The axis below the bar shows approximate time as millions of years ago (Ma). The colour shading of the bar shows the climate regime in five categories. Figures inside the bar show the number of studies analysed from each period. Examples of clades are inserted: ciliates as a group derive from the coldest period of earth, around 600 Ma, gastropods evolved c. 500 Ma during the warm Cambrian explosion; stomatopods (mantis shrimp) evolved c. 330 Ma on a relatively cold planet, swallowtail butterflies evolved c. 50 Ma in a much warmer climate. The basic morphological appearance, and probable environmental preferences, of these organisms have remained relatively unchanged since initiation of the respective clades. Each group today shows tropical affinities or non-affinities that are in accordance with the climate at their origin. Photo credits: David R. Nash (gastropod and swallowtail), Jens T. Høeg (ciliate), Roy L. Caldwell (stomatopod).

**Table 1** The pre-historic ages and their associated climate. Age is the traditionally ascribed geological period. The second column shows the date spans of the pre-historic ages in millions of years ago (Ma). The third column shows the climate trend within the period. The fourth column indicates the Palaeoclimatic category as designated in this study, consisting of five categories ranging from coldest (category 1; snowball earth') to the warmest (category 5; 'warm').

Age	Date (Ma)	Climate trend	Palaeoclimatic category	Sources
Precambrian	750–590	'Snowball earth'	1	Ruddiman (2001)
Early Cambrian	590–570	Warming	2	Estimated*
Early Cambrian	570–550	Warming	3	Estimated*
Cambrian–Devonian	550–359	Warm	4	Ruddiman (2001)
Tournaisian–Visean (Carboniferous)	359–326	Beginning glaciation	3	Dimichele <i>et al.</i> (2004)
Serpukhovian (Carboniferous) –Sakmarian (Permian)	326–293	Full glaciation	2	Scheffler <i>et al.</i> (2003), Dimichele <i>et al.</i> (2004)
Sakmarian–Lopingian (Permian)	293–240	End glaciation	3	Crowell (1982), Scheffler <i>et al.</i> (2003), Dimichele <i>et al.</i> (2004)
Triassic–Jurassic	240–170	Pangaea, arid, warm	4	Crowell (1982), Dimichele <i>et al.</i> (2004)
Late Jurassic	170–145	Cooler	3	Ruddiman (2001)
Early Cretaceous	145–135	Warming	4	Estimated*
Cretaceous–Eocene (Tertiary)	135–48	Warmest	5	Douglas & Woodruff (1981), Savin (1982), Ruddiman (2001)
Eocene (Tertiary)	48–38	Cooling	4	(Douglas & Woodruff (1981), Savin (1982), Kennet (1995), Ruddiman (2001)
Oligocene–Miocene (Tertiary)	38–14	Glaciation	3	Douglas & Woodruff (1981), Savin (1982), Kennet (1995)
Miocene–Pliocene (Tertiary)	14–0	Full glaciation	2	Douglas & Woodruff (1981), Savin (1982), Kennet (1995)

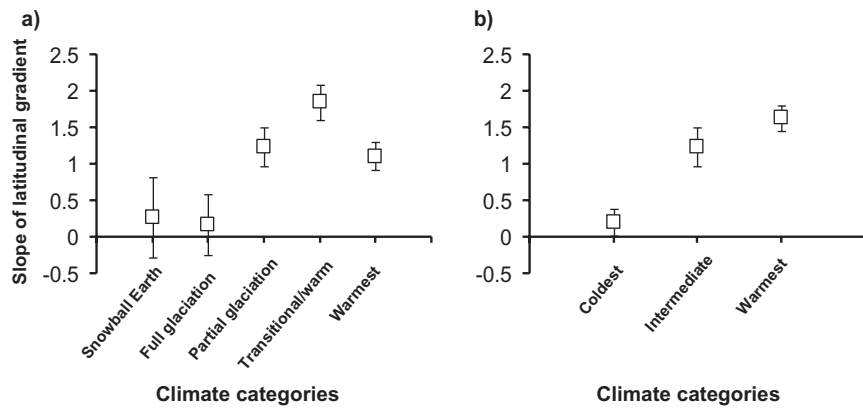
\*Transitional intervals as estimated by the authors.

## RESULTS

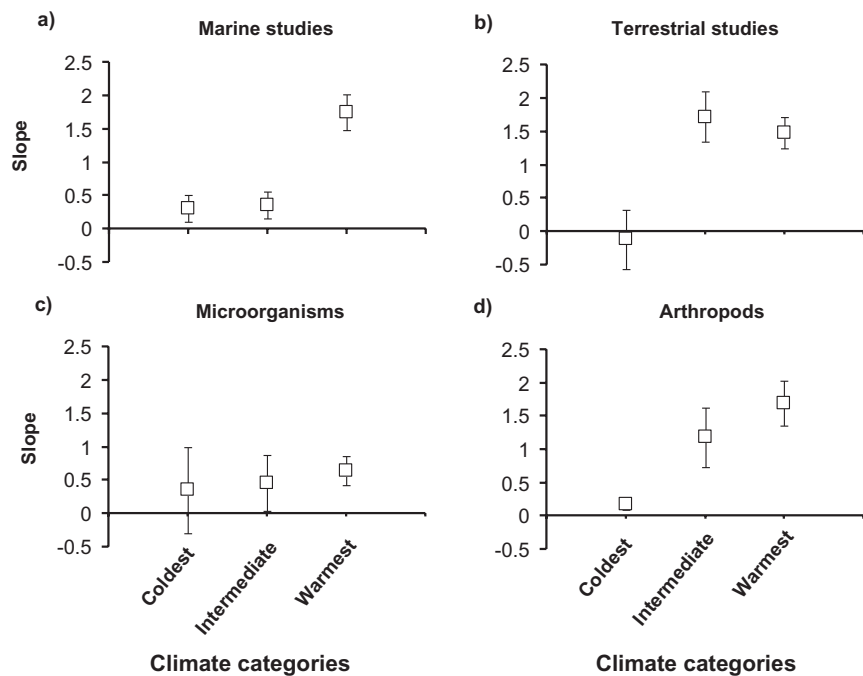
Latitudinal gradients of diversity between clades originating in different climate categories were significantly different from each other (Kruskal–Wallis test:  $n = 343$ ,  $H = 10.00$ ,  $P < 0.05$ ). Clades originating during relatively cold climatic periods, i.e. 'snowball earth' and 'full glaciation', exhibited weak to non-existent present-day latitudinal gradients in clade richness

(Fig. 2a). Clades originating during 'transitional/warm' periods have steep latitudinal gradients, although clades originating in the warmest periods have a relative shallower latitudinal gradient (Fig. 2a). Due to the small number of studies available for cold periods we compared only cold versus intermediate versus warm climates (i.e. grouping the original five categories into three categories by combining the two coldest and two warmest categories). Differences between latitudinal diversity slopes of

**Figure 2** Mean slope of the latitudinal gradient in species richness for clades originating under different palaeoclimatic regimes throughout the history of earth when the 343 studies are divided into five and three climate categories, respectively. Error bars indicate standard errors of the means. (a) Studies grouped in five palaeoclimatic categories; (b) the same studies combined into three palaeoclimatic categories.



**Figure 3** Mean slope of the latitudinal gradient in species richness for different functional and taxonomic subgroups originating under different palaeoclimatic regimes throughout the history of earth. Error bars indicate standard errors of the means. Studies are organized into three palaeoclimatic categories: (a) all marine studies, (b) all terrestrial studies, (c) microorganisms, and (d) arthropods.



clades when grouped into these three categories were significant overall (Kruskal–Wallis test:  $n = 343$ ,  $H = 8.74$ ,  $P < 0.05$ ; Fig. 2b) as well as between the coldest and warmest categories (pairwise Wilcoxon rank test:  $n = 255$ ,  $Z = 2.746$ ,  $P < 0.01$ ). The trend for clades originating during cold climatic periods to exhibit weak latitudinal gradients applies to groups as diverse as macrolichens, mosses and isopods, as well as groups that arose in either of the two pre-historic glacial periods (see also legend of Fig. 1).

When examining data in ecological and taxonomic subgroups, we found that latitudinal gradients in richness for clades pertaining to the marine realm were significantly steeper for groups that originated in the warmest palaeoclimates than for others (Kruskal–Wallis test:  $n = 176$ ;  $H = 10.21$ ,  $P < 0.01$ ; Fig. 3a). For terrestrial organisms the same trend was observed (Fig. 3b), but neither overall differences (Kruskal–Wallis test:  $n = 167$ ;  $H = 3.46$ ,  $P < 0.2$ ) nor pairwise test differences were significant. We found that microorganisms, including Bryozoa, Protista, rotif-

ers, diatoms and ciliates, exhibited a weak trend in the slope of latitudinal gradient in clade richness among different palaeoclimatic categories (Kruskal–Wallis test:  $n = 43$ ,  $H = 1.31$ ,  $P < 0.6$ ; Fig. 3c). In contrast, arthropods (including amphipods, copepods, isopods, decapods, ants, bees, termites and butterflies) conformed strongly to the overall pattern (Kruskal–Wallis test:  $n = 92$ ,  $H = 12.51$ ,  $P < 0.01$ ; Fig. 3d).

## DISCUSSION

Most clades originated during warm periods, as exemplified by the Cambrian ‘explosion’ of marine phyla and the Mesozoic radiation of vertebrates and plants (Benton, 1993). The greater the time and the area available for diversification in the tropics the greater the expected size of the species pool with tropical affinities. Higher diversification rates in warmer climates would also accentuate the tendency for a larger pool of lineages with

tropical affinity. The niche conservatism hypothesis proposes that the majority of extant organisms have retained a tropical affinity, because climatic niches of entire clades are not readily changed. Of course, it is not easy to disentangle hypotheses explaining the formation of the pool of species and hypotheses explaining its geographical distribution, because both mechanisms predict coincident diversity gradients. However, niche conservatism can be invoked to explain why warm-initiated clades tend to be associated with steep latitudinal gradient with peaks in clade richness toward the equator, whereas cold-initiated clades do not. If conservatism of climatic niches did not exist, clades that originated under particular climatic conditions in deep time would be expected to have been able to colonize and adapt to areas with different conditions today.

In our analysis a few departures from the predictions arising from niche conservatism were detected. Microorganisms revealed only a weak diversity gradient. This is in accordance with the current perception of microorganisms having idiosyncratic distributions and not conforming to many general biogeographical patterns (Fenchel & Finlay, 2009). The observation that the latitudinal gradient in clade richness for the warmest climate category is less steep than for the next warmest (Fig. 2a) is another exception. We propose this might be due to the excessive desiccation of terrestrial habitats, predominant on much of the planet in the very warm Jurassic and Cretaceous periods (Ruddiman, 2001). Earth's warm and dry habitats today are mainly situated at 20–40° of latitude, having a slight adverse effect on the richness gradient of dry-habitat organisms, such as some reptile groups (M.B.A., unpublished data). These exceptions call for further research as they may help tease apart competing hypotheses that make predictions of patterns that coincide spatially.

Even though individual species can adjust their environmental niche and adapt to new conditions, the majority of lineages in our study exhibited latitudinal diversity slopes that are in accordance with expectations of the tropical niche conservatism hypothesis given that most lineages have retained affinities to their ancestral niche. One striking example is the New World marsupials, where only a single species, the Virginia opossum, has colonized North America (Willig & Lyons, 1998; Romdal *et al.*, 2005). Our study constitutes a global multiclade test of the tropical niche conservatism hypothesis and offers empirical evidence in support of it. We have now shown that the relatively few groups in our data that originated under colder conditions have retained an overall insensitivity to present-day latitudinal gradients in climate. The question arises why so few clades appear to have originated in colder periods, given that these periods extend over a considerable proportion of the last 750 million years (Fig. 1). One explanation is that there has only been a single glacial period between 550 and 20 Ma, whereas tropical conditions have predominated throughout most of the period during which multicellular organisms have evolved (Fig. 1).

Whereas ecological explanations for the latitudinal diversity gradient have dominated the literature in the past 20 years, evolutionary mechanisms are now gaining momentum (Hawkins *et al.*, 2007; Mittelbach *et al.*, 2007; Ricklefs, 2007;

Araújo *et al.*, 2008). Studies have shown that tropical species tend to be older than extra-tropical ones, in accordance with the view that the tropics may have acted as a 'museum' of biodiversity, due to lower extinction rates (Gaston & Blackburn, 1996; Hawkins *et al.*, 2007). The tropics also hold greater variation in clade age, in accordance with a view that they may have acted as a 'cradle' of extant diversity (Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007; Weir & Schluter, 2007). Simulations have shown that an evolutionary process involving niche conservatism can give rise to diversity patterns that are very similar to those arising from empirical data (Rangel *et al.*, 2007). In parallel, the results of empirical studies have been interpreted in accordance with the expectation of the tropical niche conservatism hypothesis for continental and global distributions of birds (Gaston & Blackburn, 1996; Hawkins *et al.*, 2005, 2006, 2007). In other taxon-specific analyses, current global tree species diversity across different bioclimatic regions correlated with the integrated area of each region over the last 55 million years (Fine & Ree, 2006), and geographical origination has been shown to be decisive in predicting the strength of latitudinal diversity gradients in bivalves (Krug *et al.*, 2007), major groups of frogs (Wiens *et al.*, 2006, 2009) and mammals (Buckley *et al.*, 2010). In comparison, the present-day diversity gradient for all frogs and salamanders appears to be largely created by a higher diversification rates in the tropics (Wiens, 2007). Although the pattern might be affected by a larger extent of the tropics being responsible for creating higher diversification rates in ancient tropical clades (Wiens, 2007), discernible signals have been identified among climatic niches of all groups (Hof *et al.*, 2010).

Several of these studies are in accordance with both the niche conservatism and the diversification rate hypotheses. In fact they appear not to be mutually exclusive. Both hypotheses, as well as ecological hypotheses linked to differing carrying capacities of climate zones relative to the solar input of energy and water balance (Currie *et al.*, 2004; Hawkins *et al.*, 2005; Whittaker *et al.*, 2007), may act in concert to enhance the tropical diversity peak. However, niche conservatism makes no a priori assumption with respect to diversification rates or ages of clades (Wiens & Donoghue, 2004). The crux of the niche conservatism hypothesis for understanding global diversity is simply that more clades are adapted to tropical climates because of the larger integrated area of the tropics over time. The hypothesis is therefore independent of the debate as to whether the tropics have been a 'museum' (low extinction rates) or a 'cradle' (high speciation rates) for current biodiversity. Our analysis has revealed a pattern that is in accordance with the signature of niche conservatism over a time period of hundreds of millions of years on the present-day pattern of global diversity. For current distributions of both ancient as well as more modern lineages, we found significant differences in the shape of the latitudinal gradient of species richness among clades. These results provide evidence of a lasting influence of the climate at clade initiation, with the consequence that the extant tropical diversity peak is created from lineages that adapted to a planet with tropical climate. This may also serve as a caution that large-scale changes in climate patterns, even when developing



subtly over millions of years, leave a massive and irreversible signature on the most prominent of diversity patterns.

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## SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article at the publisher's web-site.

**Table S1** Full list of gradient studies used in analyses.

## BIOSKETCHES

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