Global-scale episodes of transoceanic biological dispersal during the Cenozoic

Daniel Viete (✉ viete@jhu.edu)

  Johns Hopkins University

Siobhán Cooke

  Johns Hopkins School of Medicine

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1 **Global-scale episodes of transoceanic biological dispersal during the Cenozoic**

2 Daniel R. Viete[1] & Siobhán B. Cooke[2]

3 1. Department of Earth & Planetary Sciences, Johns Hopkins University; 2. Center for

4 Functional Anatomy & Evolution, Johns Hopkins School of Medicine

5 **Since formalization of plate tectonic theory in the 1960s, vicariance has been the**

6 **dominant model for interpretation in biogeography. However, modern research**

7 **suggests transoceanic 'rafting' is also an important process in biological dispersal.**

8 **Here we show that Cenozoic occurrences of rafting-associated colonization of new**

9 **lands by terrestrial biota are not randomly distributed in time, but cluster at c. 40**

10 **million years ago (Ma) and c. 15 Ma. These excursions in rafting activity are reflected**

11 **across taxonomic groups and ocean basins. The global scale and ~25 million-year (My)**

12 **wavelength of the fluctuations suggest they are associated with planetary-scale**

13 **changes and/or events.**

14 Simpson [1] argued that differences in the terrestrial faunal assemblages of Africa and

15 Madagascar could be explained by an adventitious process of faunal exchange; migration

16 from Africa was limited to fauna whose physiology could, on rare attempt, allow survival of an

17 extended oceanic journey then establishment of a viable Malagasy population. With the rise

18 of dated molecular phylogenetics as well as advances in geologic/tectonic reconstructions

19 and quantitative paleontology/stratigraphy, it is now thought that much of Madagascar's

20 unique terrestrial fauna accumulated as the result of oceanic dispersal [2–4]. Rafting events

21 resulting in successful colonization of a new land, N_S, are related to number of rafting

22 'attempts', N_A, by some probability of success, p, which is a product of the probabilities of the

23 various requirements for establishment of a new population (p_1, p_2, p_3 … p_n), including

24 surviving the journey, new environment suitability, availability of appropriate niches, sufficient

25 genetic diversity in the colonizing population, etc.:

26 $$N_S = N_A \cdot p = N_A \cdot \prod_{i=1}^{n} p_i \qquad\qquad\qquad \text{Equation 1}$$

27 Accumulation of N_A can involve relatively frequent, small-scale triggers (e.g., storm

28 events) and/or less frequent, larger-scale triggers (e.g., ocean-scale tsunami). The chances of

29 rafting success involve probabilities that are dependent on how N_A accumulates—e.g., a large

30   event (or series of events) that cast more individuals out to sea may improve chances of

31   sufficient population numbers and genetic diversity at the arrival point. In addition to non-

32   linearities arising from feedbacks among triggering magnitude/frequency and p, some of the

33   individual probabilities, p_i, of Equation 1 will change (locally or globally) over geologic time;

34   ocean size, circulation patterns and the distribution of island arcs/oceanic islands vary in

35   response to tectonics and changing climate/sea level.

36   How might chance of success in the 'oceanic dispersal sweepstakes' vary with the

37   timing and/or size of the draw? We consider the timing of Cenozoic colonization events that

38   can be confidently associated with oceanic dispersal of terrestrial biota, and whether rafting

39   activity may fluctuate/cluster on geologic time scales. Specifically, we consider all published

40   accounts of rafting events between the start of the Campanian and end of the Miocene (84–5

41   Ma; older cut off chosen to ensure inclusion of events within uncertainty of the Cenozoic,

42   younger to reduce likelihood that anthropogenic dispersal events were considered). Cenozoic

43   tectonic events relevant to dispersal among landmasses (with plate reconstructions at 80, 60,

44   40 and 20 Ma) and spatiotemporal constraints on dispersal events associated with rafting are

45   summarized in the Supplementary Material.

46   Our compilation includes dates obtained by penalized likelihood [5] (n=54) and

47   Bayesian relaxed molecular clock [6–7] (n=215) approaches, in addition to direct fossil

48   constraints (n=2). Modern, fossil-calibrated, variable-rate molecular clock approaches are

49   imprecise [8]. They also suffer from systematic biases, particularly when calibration points are

50   few and/or limited genes are considered [9]; associated accuracy issues may result in

51   systematic shifts/stretches in time estimates. Imprecision introduces noise to the compilation

52   and may mask distinct events at the My time scale. However, any statistically-significant

53   clustering of rafting activity at >5–10 My time scales should be apparent and will not reflect

54   uncertainty in the data. The goal in compiling was therefore to obtain sufficient sample size to

55   make statistical assessments, and our inclusive approach considered all credible, peer-

56   reviewed work published since 2000. In the absence of firm author recommendations,

57   evolutionary divergence was associated with dispersal (founder-event speciation [10]), and

58   timing of rafting was taken as the age of the last common ancestor to the most-closely related

59   biota among the original and colonized landmasses. Additional details on approaches used in

compilation and statistical analysis of the dataset are in the Methods. The full rafting event
compilation is provided in the Supplementary Material.

Figure 1 provides histograms and kernel density estimations (KDEs) for vertebrates, all
animals (vertebrates plus arthropods) and all animals plus plants. The vertebrates histogram
(Fig. 1A) shows potential clustering at c. 72 Ma, c. 41 Ma and c. 19 Ma, but the earliest and
latest potential clusters are masked by large-bandwidth KDE smoothing due to low data
density; an adaptive KDE with bandwidth 5 My resolves all three populations (Fig. 1A). When
the arthropod events are added, the automated-smoothing-bandwidth KDE routine yields
peaks at c. 67 Ma, c. 40.5 Ma and c. 18 Ma (Fig. 1B). The addition of plants to the analysis
further emphasizes the youngest peak (Fig. 1C). Lower-rafting-frequency windows at c. 60–
50 Ma and c. 30–20 Ma are apparent for all taxonomic groupings (Extended Data Fig. 1);
Kolmogorov–Smirnov tests support non-random distribution for the various datasets at
confidence intervals of 92.8%, 95.9% and 99.6% for vertebrates, arthropods and all animals,
respectively, and >99.99% for all plants and all taxa. Resolved peaks (and troughs) are all
inboard of the distribution end points by multiple smoothing bandwidths (>>5 My), suggesting
limited influence of boundary effects on their position [11].
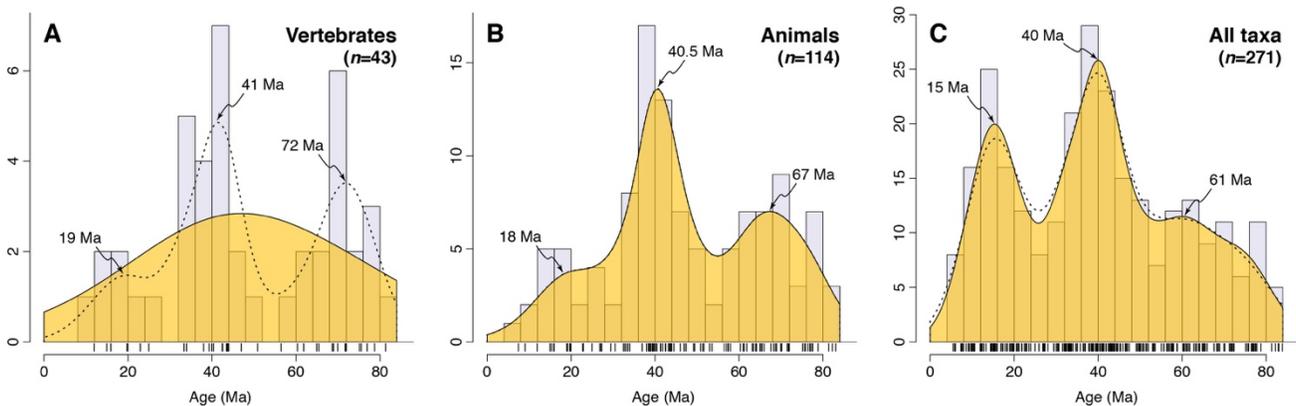
Figure 1. Histograms (4 My bins) and KDEs (default smoothing [12]; 5 My smoothing provided
as dotted trace) for all data for: (A) vertebrates; (B) vertebrates plus arthropods; (C) animals
plus plants. Ages of peaks are shown. Extended KDE plots are provided in the
Supplementary Material.

Figure 2 shows histograms and KDEs using a 5 My smoothing bandwidth—
approximately corresponding to values for automatically-selected smoothing bandwidths [12] in
the large-n KDEs for 'all animals' (Fig. 1B), 'all plants' and 'all taxa' (Fig. 1C)—for all rafting

84   events for the Atlantic Ocean (Fig. 2A), Indian Ocean (Fig, 2B), and Pacific and Southern

85   Oceans (Fig. 2C). Peaks in rafting frequency are shared across ocean basins; middle Eocene

86   (c. 40 Ma) and middle Miocene (c. 15 Ma) peaks are resolved for all three regions, and

87   Cretaceous–Paleogene (c. 66 Ma) peaks are apparent for the Indian and Pacific/Southern

88   Oceans.

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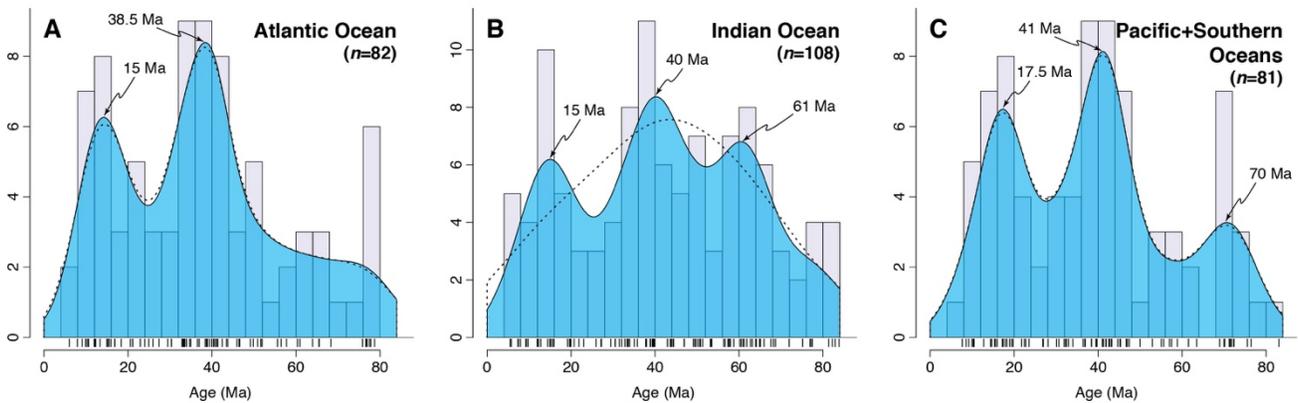
Figure 2. Histograms (4 My bins) and KDEs (5 My smoothing; default smoothing [12] provided
as dotted trace) for all data from: (A) the Atlantic Ocean; (B) Indian Ocean; (C) Pacific and
Southern Oceans. Ages of peaks are shown. Extended KDE plots are provided in the
Supplementary Material.

94   Analysis of the temporal distribution of Cenozoic rafting reveals enhanced activity at c.

95   40 Ma, c. 15 Ma, and potentially also c. 67 Ma (among animals in particular). These ~25 My-

96   wavelength fluctuations are recorded across multiple taxonomic groups and all major extant

97   ocean basins.

98   The earliest and least confidently resolved of the enhanced rafting episodes coincides

99   (within uncertainty) with the Cretaceous–Paleogene mass extinction event. The c. 67 Ma

100   excursion in rafting activity may therefore potentially record enhanced opportunities for

101   colonization following die-off of competing life forms [13]. However, the better-resolved c. 40

102   Ma and c. 15 Ma episodes have no obvious associated extinction events, and are not simply

103   explained by widespread removal of biological barriers to colonization. Changes in ocean size

104   (continental/island arc arrangements) and/or oceanic circulation patterns could account for

105   geologic-wavelength variation in rafting activity in certain regions and directions [4]. However,

106   the enhanced rafting episodes retrieved from our analysis are global (Fig. 2), and are thus

107   also difficult to explain simply by changes in the spatial pattern of processes. The c. 40 Ma

108   and c. 15 Ma episodes are coincident with the Middle Eocene and Middle Miocene Climatic

109   Optima [14], meaning that enhanced rafting activity cannot be linked to glaciation-related sea

110   level drop, and associated coastline regression and/or appearance of oceanic island refugia,

111   but may point to an enhanced likelihood of rafting success, p, during these warmer periods

112   when more suitable habitat would have been available for tropical species to colonize.

113   Clustering across taxa and oceans suggests fluctuations cannot be simply associated with

114   stochastic emergence of particularly adaptable lineages (sweepstakes ticketholders).

115   Alternative explanations for global fluctuations in rafting activity may lie in triggering,

116   and modification of rafting attempts, N_A, and/or the influence that mode of accumulation of N_A

117   may have on p. The effects of changing climate on the frequency, intensity and distribution of

118   storm events is highly non-linear [15], and the middle Eocene and middle Miocene hothouse

119   Earth events [14] may have led to considerable changes in rates of accumulation of N_A,

120   globally. Deformation at ocean margins involves large subduction-zone earthquakes and

121   tsunami, and varies over geologic time scales in response to tectonic changes, including plate

122   reorganization events [16]. For example, the biological effects of the 2011 Tōhoku earthquake

123   and tsunami included dispersal of more than 289 species of coastal marine biota from the

124   Japan region around the Pacific Ocean [17]. Large meteorite impacts with average frequency

125   $10^{-6.5}$–$10^{-7.5}$ y^{-1} have kinetic energy that could exceed that released in the Tōhoku earthquake

126   by a factor of 10^3–10^6 [18]. The majority of meteorite impacts should be located in ocean

127   basins, and large impacts may produce massive tsunami, yet leave only cryptic records of

128   their occurrence [19].

129   Colonization of South America by African ancestors of the platyrrhine monkeys and

130   caviomorph rodents in the middle Eocene [20] did not involve a few individuals one day

131   deciding to swim west; dispersal was likely triggered by catastrophic circumstances that saw

132   countless individuals cast far into the Atlantic Ocean. Could large events such as rapid

133   climate change or basin-/global-scale tsunami (clusters) not only result in biological

134   destruction, but assist biological dispersal and radiation by rafting? Could planetary-scale

135   processes operating on geologic time scales exert strong influences over biological dispersal

136   in manners that transcend vicariance?

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AUTHOR CONTRIBUTIONS: According to the CRediT taxonomy: Viete—conceptualization, data curation, formal analysis, methodology, visualization, writing (original draft); Cooke— data curation, validation, writing (review and editing).

COMPETING INTERESTS: The authors declare no competing interests.

ADDITIONAL INFORMATION: Supplementary Information is available for this paper, including: (1) Tectonic constraints used to identify transoceanic dispersal events; (2) Extended KDE plots; (3) Compiled dataset. Correspondence and requests for materials should be addressed to Daniel R. Viete.

METHODS:

Our approach considered rafting events involving vertebrates (n=43), invertebrates (arthropods; n=71) and plants (mainly angiosperms, some ferns; n=157). Only biota from continental environments were considered. Fish, bats and birds were excluded, in addition to eusocial (Isoptera, Apidae, Cabronidae, Formicidae, Halictidae, Vespidae) and migratory insects (Lepidoptera, Orthoptera, Odonata). Analysis of the temporal distribution of rafting activity was performed using a non-parametric, kernel density estimation (KDE) approach.

Smoothing of the KDE used an adaptive method that adjusts the smoothing bandwidth according to data density [1]. Where not otherwise stated, optimal smoothing bandwidth was calculated from the data following the approach of Botev et al. [2]. Potential boundary effects were not corrected for, but are expected to be significant only for regions within a smoothing bandwidth of the distribution end points [3–4]. All plotting and visualization used the online program IsoplotR [5].

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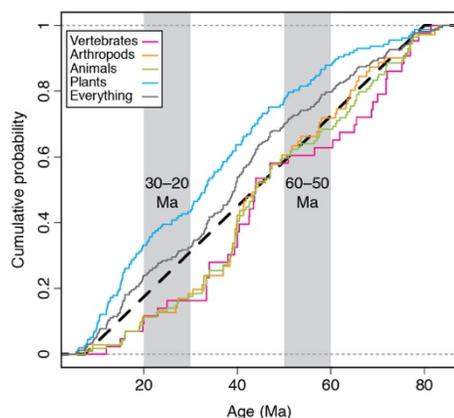
EXTENDED DATA FIGURE:

Extended Data Figure 1. Cumulative probability curves for groupings in manuscript Fig. 1A–C, in addition to just arthropods and just plants. Gray bands highlight time periods with relatively few rafting events. Dashed line illustrates a random distribution.
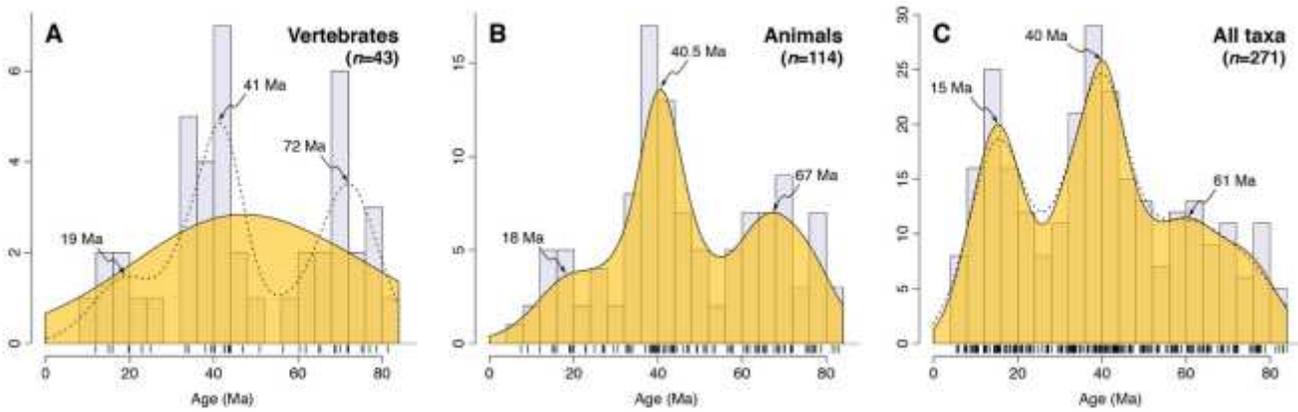
Figures

Figure 1

Please see the manuscript file to view the figure caption.
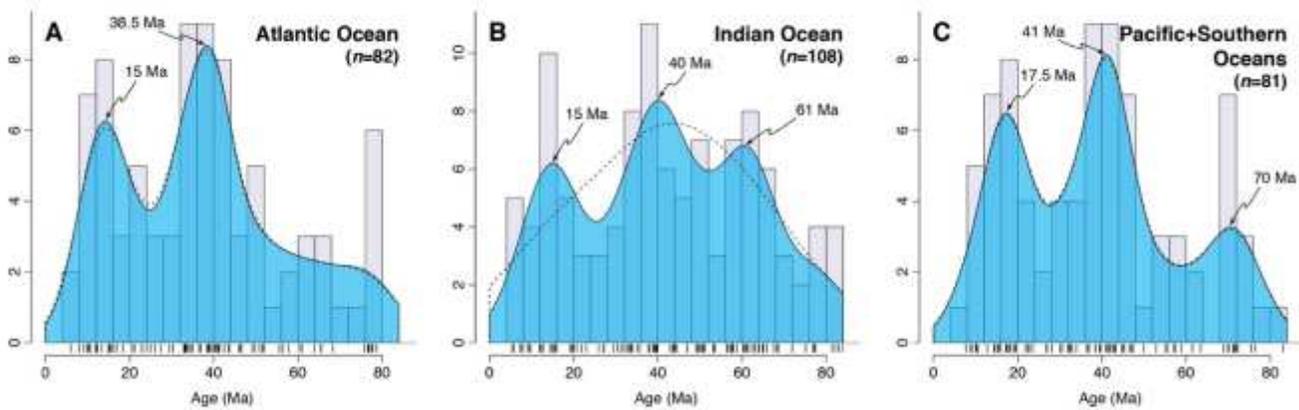

Figure 2

Please see the manuscript file to view the figure caption.

Supplementary Files

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- ExtendedKDEplots.pdf
- TectonicsSupplement.pdf