Global long-term stability of individual dietary specialization in herbivorous mammals

Larisa R. G. DeSantis, Melissa I. Pardi, Andrew Du, Michael A. Greshko, Lindsey T. Yann, Richard C. Hulbert and Julien Louys

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Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History
RSPB-2021-1839.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No
Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?  
Yes

Is it clear?  
Yes

Is it adequate?  
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
Please see my comments in the attached PDF (Appendix A).

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Acceptable

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?  
Yes
This manuscript analyzes a dataset of stable carbon isotope serial samples from mammalian herbivore dentitions to ask whether ‘dietary generalism’ in a species emerges from intra- or inter-individual dietary variation. They find that most generalist species are comprised of individual specialists, with grazers showing the highest levels of individual variation (based on the authors’ isotopic individuality index).

This is an interesting ecological question, but it has been addressed in previous work as noted in the introduction. Nonetheless, this study’s synthesis of existing stable isotope data in the literature and inclusion of new samples from C3-C4 mixed-feeding taxa is a nice addition to the existing literature. I have a few comments/questions for the authors to consider.

Major Comments
Isotopes are a proxy for diet and record dietary information over specific time scales. There is surprisingly no discussion of how dental maturation rates across taxa relate to serial samples, given the fact that sampling rates and distances vary, in addition to fundamental differences in the dental biology of taxa analyzed. The authors consider variation in crown height (and use a five-sample sliding window in an attempt to control for this) but should also discuss how variation in the timing of the individual’s life is reflected in serial samples — Are all samples considered to be annual, semi-annual? Does this vary across taxa? Does it matter? Without these considerations, the manuscript feels incomplete.

I ask these questions because depending on the scale of diet information recorded, you could have a scenario where a dietary generalist looks like a specialist (from the view of isotopes) because of temporal averaging of isotope signals. We all acknowledge that bulk samples record average diet, but even serial samples are averaging diet over a certain span of time. If that span of time systematically varies across taxa, that adds a major complication. For example, could greater intratooth δ13C range in grazers reflect faster dental maturation times due to taller crowns and thus less temporal averaging of isotopic variability?

How does consideration of variation in plant isotopic composition impact these conclusions? For example, Cerling and others have discussed differences between NADP and NAD+PEP-CK grasses in the African context. Could systematic differences in isotopic variability between browse and graze impact your findings?

Minor Comments
pg 7, line 217-220: But what about time in terms of the osteological collections? A lot of museums house collections that were collected across several decades, if not centuries, and probably sample sporadically across a species’ geographic distribution. Could species dietary niches shift on those scales?

pg 9, line 382: “Individuals identified to the genus level were lumped with congener individuals identified to the species level when it could be reasonably inferred that they belonged to the same
species (e.g., Mammuthus sp. lumped with Mammuthus columbi)” – does this vary by feeding group? Could unidentified species be inflating genus level variation?

Decision letter (RSPB-2021-1839.R0)

18-Oct-2021

Dear Dr DeSantis:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers’ comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under “Manuscripts with Decisions.” Under “Actions”, click on “Create a Revision”. Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers’ and Editors’ comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as ‘tracked changes’ to be included in the ‘response to referees’ document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

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If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

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If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data).Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Thank you for your submission. Both reviewers agree that the dataset is strong and that this will make a positive contribution to the literature, although they both have concerns that will need to be addressed before the paper can be accepted. These include Reviewer 1’s concerns regarding the pre-assignment of species into body size groups prior to statistical comparisons—additional justification of this approach will be necessary. Also, Reviewer 2 suggests that greater care be taken to place these conclusions within the context of prior work, as the main conclusions are not entirely novel.
The statistical methods are relatively straightforward and generally adequate. My only concern with their analyses are not with the stats itself, but with the pre-assignment of species into body size groups before making statistical comparisons among them. The assignments appear to be somewhat arbitrary, and I think some justifications (perhaps in the supplementary material) would be needed.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
Please see my comments in the attached PDF.

Referee: 2
Comments to the Author(s)
Review of RSPB-2021-1839 “Global long-term stability of individual dietary specialization in herbivorous mammals” by DeSantis et al.

This manuscript analyzes a dataset of stable carbon isotope serial samples from mammalian herbivore dentitions to ask whether ‘dietary generalism’ in a species emerges from intra- or inter-individual dietary variation. They find that most generalist species are comprised of individual specialists, with grazers showing the highest levels of individual variation (based on the authors’ isotopic individuality index).

This is an interesting ecological question, but it has been addressed in previous work as noted in the introduction. Nonetheless, this study’s synthesis of existing stable isotope data in the literature and inclusion of new samples from C3-C4 mixed-feeding taxa is a nice addition to the existing literature. I have a few comments/questions for the authors to consider.

Major Comments
Isotopes are a proxy for diet and record dietary information over specific time scales. There is surprisingly no discussion of how dental maturation rates across taxa relate to serial samples, given the fact that sampling rates and distances vary, in addition to fundamental differences in the dental biology of taxa analyzed. The authors consider variation in crown height (and use a five-sample sliding window in an attempt to control for this) but should also discuss how variation in the timing of the individual’s life is reflected in serial samples—Are all samples considered to be annual, semi-annual? Does this vary across taxa? Does it matter? Without these considerations, the manuscript feels incomplete.

I ask these questions because depending on the scale of diet information recorded, you could have a scenario where a dietary generalist looks like a specialist (from the view of isotopes) because of temporal averaging of isotope signals. We all acknowledge that bulk samples record average diet, but even serial samples are averaging diet over a certain span of time. If that span of time systematically varies across taxa, that adds a major complication. For example, could greater intratooth d13C range in grazers reflect faster dental maturation times due to taller crowns and thus less temporal averaging of isotopic variability?

How does consideration of variation in plant isotopic composition impact these conclusions? For example, Cerling and others have discussed differences between NADP and NAD+PEP-CK grasses in the African context. Could systematic differences in isotopic variability between browse and graze impact your findings?

Minor Comments
pg 7, line 217-220: But what about time in terms of the osteological collections? A lot of museums house collections that were collected across several decades, if not centuries, and probably sample sporadically across a species’ geographic distribution. Could species dietary niches shift on those scales?
Individuals identified to the genus level were lumped with congener individuals identified to the species level when it could be reasonably inferred that they belonged to the same species (e.g., Mammuthus sp. lumped with Mammuthus columbi). Does this vary by feeding group? Could unidentified species be inflating genus level variation?

Author's Response to Decision Letter for (RSPB-2021-1839.R0)

See Appendix B.

Decision letter (RSPB-2021-1839.R1)

10-Jan-2022

Dear Dr DeSantis

I am pleased to inform you that your manuscript entitled "Global long-term stability of individual dietary specialization in herbivorous mammals" has been accepted for publication in Proceedings B. Congratulations!!

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Data Accessibility section
Please remember to make any data sets live prior to publication, and update any links as needed when you receive a proof to check. It is good practice to also add data sets to your reference list.

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Electronic supplementary material: All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Dr John Hutchinson
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
The current version of the manuscript is improved, and does a better job placing the current study in the context of prior work. The dataset assembled here is impressive and will influence the future direction of palaeoecological, and present-day ecological studies on intraspecific variation in diet.
Appendix A

General comments:

This study provides insights into the topics of niche theories, isotope ecology, and dietary evolution. The compilation of published serial sample data, along with newly collected data, are a valuable contribution to the field. This well-curated database is potentially useful for many future studies.

The paper investigates interesting questions about individual specialization/generalization within generalist species. The findings reveal an intriguing new phenomenon of the prevalence of individual specialists across dietary groups, shedding light into the previously lesser-known niche of “generalist specialist.”

While the study poses important research questions and has sufficient raw data for addressing the questions, I think there is still room for improvements, particularly on the following aspects:

1. I strongly recommend the authors to give more considerations to the dampening effect of the isotopic signature recorded in tooth enamel. Although this has been mentioned in the paper, the authors have not provided convincing enough evidence for why one should not be concerned about it. While I do not think this effect necessarily changes the overall conclusion of this paper (that individual specialization is a widespread phenomenon, or is at least more common that previously recognized), I do think more passages are needed to acknowledge the potential influence of the dampening of isotopic signature. Only when an individual consumes one type of plant for weeks/months in a row and then shifts to a different diet for subsequent weeks/months can the isotopic variability of its diet be faithfully recorded along the growth axis of its teeth. If an individual consumes a wide range of vegetation but does not shift its diet much seasonally, what is recorded would be the overall isotopic signature of the ingested plants, which does not fully capture the carbon isotope values and the relative proportions of the various types of plants consumed.

2. Low III in mixed feeders is primarily due to high species-level variability. Because generalist species are typically more wide-ranging than specialist species, the intraspecific variation can be a direct reflection of geographic range and vegetation availability. In other words, individual specialization within a given generalist species could reflect reduced local competition as this paper has discussed, or it could simply reflect geographic variation in plant availability and has little to do with intra- or inter-specific competition. I recommend that the authors give more consideration to the “space” element (i.e. how geographic variation in plant availability affect species-level variability and III index), especially when there are statements in the paper about how the pattern is common across space and time.

3. In addition to differentiating samples from below 37 deg latitude, it may be worth re-running some of the analyses for specimens that post-date the expansion of C4 vegetation in their respective continents.

4. I think it would be worth mentioning the range of body masses of the sampled taxa before giving the body mass bins. Because the relationship between herbivore body size and dietary ecology is rather complicated, I think if an evaluation of the effect of body size is to be done, it needs to be done carefully. Brief justifications for how boundaries between the body size bins are drawn are necessary—as of now, 100 kg and 350 kg seem to be arbitrary. Ideally, the boundary values should be of some biological or physiological relevance. If that
is the case, it needs to be explained. If the divisions are made primarily for statistical considerations (i.e. to have comparable numbers of individuals in small, medium, and large groups), this needs to be stated too.

5. Even though the mean individual ranges are generally narrow, grazers' range is ~1.6 times as wide as browsers' (and 2.4 times for <37 deg latitude), and the ranges are also significantly different between browsers and grazers (Table 1). You should talk about what this range can mean, in terms of the vegetation consumed. This would be helpful to non-specialist readers.

Additionally, the paper would also use more consistent terminology, particularly when it comes to describing dietary groups. Some in-text references to figures are incorrect—not all figures cited show what the text is talking about. Figure captions and axis labels could also be more accurate and informative. The Introduction and Discussion sections will also need some re-writing.

**Detailed comments with references to line numbers:**

37 “enamel” should be subscripted

39 maybe specify what you mean by dietary strategy by listing the three dietary groups in parentheses?

40–43 the example of *C. emsli* would probably go better with the previous sentence—that “almost all herbivores…are composed of individual specialists,” as it explains to readers clearly what you mean by individual specialists—than with the statement that this pattern holds true through time, as there is only one age associated with this example

54 “define”

55 add “choice” after “habitat”, as diet does not directly influence the physical environment per se. The rest of the sentence also needs some re-writing for better clarity. For example, I would how animals move in their environment is equivalent to migration, while migration is one aspect of landscape use and should not be mixed up with the latter.

56 Before talking about humans, say a little more about how animals’ dietary niche, especially how niche breadths have typically been defined as either broad or narrow for a certain species, then transition into how this new niche is unique

62 omit “for example”

69–71 this sentence (“In fact…”) seems to imply that such investigations have been previously done many times and revealed robust patterns

76 thought to be or found to be?

79 move “dietary” to before “specialist” to make the sentence flow better

76–81 This paragraph seems redundant to me. Basically, it is saying with examples that some generalist species are composed of generalist individuals (thereby supporting the NVH) while
many other species specialist individuals (thereby not supporting the NVH). Since this has already been stated in the previous paragraph, and carnivores are not the focus of this study, I recommend keeping only the last sentence of this paragraph.

97 before the term mixed-feeders appears here (for the first time), it is worth introducing your three dietary groups first and briefly explaining the conventional view of their dietary niche breadths

102 the duration of tooth formation is relevant and important enough here that I think there is no need for parenthesis

109–113 I recommend removing the topics of “shifts in plant species composition” and “species distributions through time” from Introduction since you did not revisit these topics in Discussion

123 I cannot tell from Figs. 1–2 that there is as much as an 8‰ range in grazers. Only Fig. 3 shows that.

125–126 What’s in parenthesis here goes better after the first sentence of the paragraph where you report the total range of carbon isotope values. Also, is it necessary to list all the countries here? Perhaps it would be better to include a map of sample locations in the supplementary file.

134 “herbivores”

160 what sampling standardization?

166–168 by “between” I think you mean “among”, since the comparisons involve more than three values

169 by “among” I think you mean “in”

176 Again, Fig. 4 does not show individual variabilities, but averaged individual variabilities. The 8‰ range mentioned in this sentence is not shown in Fig. 4.

188–189 morphologically “and nutritionally” constrained; would also be good to include citations here about browsing species’ constraints

190–191 I’d be curious to see what their serial sample profiles look like, perhaps it would be worth graphing them (like what is done for C. embliiei in Fig. 2) in the supplementary file

200–216 The argument in this paragraph is relatively weak. The fact that different parts of grass forage do not get selected upon as finely as the architectural heterogeneous browse materials would contribute to higher isotopic variability in grazers only if the different parts of grasses have highly variable isotopic signatures, and I'm not sure if that’s the case. I think how feeding selectivity translates to isotopic variability is a little more complex than what is described here. Note that there is greater variability in the C₃ plants than in C₄ plants, and when grasses are consumed as a whole, only one overall isotopic signal is recorded in the teeth regardless of how much variability is among the plant parts. Additionally, the second sentence (tradeoffs for consuming grasses) and the last sentence (mixed feeders having the lowest III indices) of this paragraph seem out of place. Their logical linkage to the rest of the paragraph is not strong. You need to write elaborate on both statements if you keep them where they are.
While time averaging does not affect what you found for individual teeth (Figs.1-3), you may want to consider how it may affect your calculated III indices (Fig. 4). In other words, the III values of extinct taxa are potentially lowered by the effect of time averaging.

this “example” does not match what you just talked about…it is critical in this paper to address the dampening effect of recorded isotopic signatures, and to make a sound argument here you need examples of a single tooth recording a wide range of carbon isotope values

I am a little bothered by “there is no reason why…”, as you are trying to give an example to support an argument. The absence of evidence is not the evidence of absence.

Sentence in parenthesis is a little redundant

what roles?

These two sentences are a bit confusing. First, you talk about individuals consuming disparate foods, which to me implies more generalist individuals, then you talk about individual specialization in the second sentence. Perhaps you can modify the phrasing in the first sentence.

what do you mean by “extreme”? is there a reason to emphasize on extreme generalists (as opposed to other, less extreme generalists) here?

Fig. 4 does not indicate age, nor are taxon ages noted in the supplement

Comments on figures and tables:

In all figures the Y-axis label should include “enamel” to match the text, and the unit should be in parenthesis, making it: $\delta^{13}C_{enamel}$ (‰)

Figure 1

“breadths”

“if individuals have more specialized (left) or more generalized (right) diets”

This figure is very intriguing and informative, with theoretical predictions (left and middle columns) and empirical results (right column) shown simultaneously. It is probably the one figure that best summarizes the key findings of this study, and so it would be good to improve it further. I have three suggestions: (1) Symbols in figure legend should match the colors in the graph, since each symbol (species) only has one corresponding dietary assignment (color). (2) In the figure caption, it would be worth noting that tooth crown height generally increases with higher levels of grazing. (3) It is not clear to me why these six taxa are chosen as examples to be presented here. Why not illustrate the entirety of your dataset?

Figure 2
“(range = 13.4‰)”

564–565 just say “browsers” and “grazers” since (1) “obligate” is not defined or used elsewhere in the paper, and (2) in the literature, obligate grazers are distinguished from variable grazers and have quantifiable defining criteria, so do not mix up grazers with obligate grazers if what you really mean here is grazers

Figure 3
569–570 end members of a range should have the same number of decimal places

570 not clear to me what you mean by “methods”

For each panel, give the sample size (numbers of individuals) of the dataset (n = #). Avoid using “trophic group” in Y-axis labels, since you don’t use these words anywhere else in the paper. Just say “dietary category.” I would also remove “Individual Isotopic Variability” from the panel headings, since they are all the same, and incorporate the phrase into figure caption if necessary.

Figure 4
Panels A) and C) need more informative Y-axis labels (add “species” to Y axis to contrast the “average individual” on X axis)

I don’t really see what you describe about panel C)—that species in low latitudes plot close to the 1:1 line than other species.

Figure caption should include explanation for the box and whisker plots; alternatively, add an inset diagram to panel B) or D).

Table 1
To my understanding, “n” denotes number of individuals for range (top half of the table) and number of species for III (bottom half of the table). If so, the abbreviation explanation should be corrected at the bottom of the table.
Dear Associate Editor John Hutchinson:

Thank you for your consideration of this manuscript. Based on the reviews, all reviewers have commented on the importance of this data set and the conclusions drawn from these data. Two primary comments were made: 1) the need to address the body size categories used (i.e., why these categories were used prior to a statistical analysis), and 2) the need to better link the conclusions of this paper with prior work. We appreciate these comments and agree that an improved discussion of both topics is important. We have made both broad and specific changes to address these and other line-item comments. We are appreciative of each of the reviewers who took the time during the COVID-19 pandemic to review this manuscript. We appreciate all their comments and feedback, and believe the resulting manuscript is stronger because of their reviews.

Reviewer #1: This study provides insights into the topics of niche theories, isotope ecology, and dietary evolution. The compilation of published serial sample data, along with newly collected data, are a valuable contribution to the field. This well-curated database is potentially useful for many future studies. The paper investigates interesting questions about individual specialization/generalization within generalist species. The findings reveal an intriguing new phenomenon of the prevalence of individual specialists across dietary groups, shedding light into the previously lesser-known niche of “generalist specialist.”

We thank the reviewer for there comments regarding the importance and value of this contribution.

While the study poses important research questions and has sufficient raw data for addressing the questions, I think there is still room for improvements, particularly on the following aspects:

1. I strongly recommend the authors to give more considerations to the dampening effect of the isotopic signature recorded in tooth enamel. Although this has been mentioned in the paper, the authors have not provided convincing enough evidence for why one should not be concerned about it. While I do not think this effect necessarily changes the overall conclusion of this paper (that individual specialization is a widespread phenomenon, or is at least more common that previously recognized), I do think more passages are needed to acknowledge the potential influence of the dampening of isotopic signature.

Only when an individual consumes one type of plant for weeks/months in a row and then shifts to a different diet for subsequent weeks/months can the isotopic variability of its diet be faithfully recorded along the growth axis of its teeth. If an individual consumes a wide range of vegetation but does not shift its diet much seasonally, what is recorded would be the overall isotopic signature of the ingested plants, which does not fully capture the carbon isotope values and the relative proportions of the various types of plants consumed.

We have now expanded the discussion of the dampening effect of the isotopic signature to specifically mention instances when an animal’s averaged diet is not fully captured if the averaged values of different sources are in similar proportion throughout time. See discussion.

2. Low III in mixed feeders is primarily due to high species-level variability. Because generalist species are typically more wide-ranging than specialist species, the intraspecific variation can be a direct reflection of geographic range and vegetation availability. In other words, individual specialization within a given generalist species could reflect reduced local competition as this paper has discussed, or it could simply reflect geographic variation in plant availability and has little to do with intra- or inter-specific competition. I recommend that the authors give more consideration to the “space” element (i.e. how geographic variation in plant availability affect species-level variability and III index), especially when there are statements in the paper about how the pattern is common across space and time.

This is a good point that we now have added to the discussion, explicitly the discussion of geographic variation in plant availability. We also do want to reiterate that this is one of the reasons we added analysis of only low-latitude specimens, so that individuals sampled occur in places were isotopic variability is possible (though of course some regional variation and potential for movement will exist, there is the potential for C3 and C4 vegetation to be consumed). See discussion.

3. In addition to differentiating samples from below 37 deg latitude, it may be worth re-running some of the analyses for specimens that post-date the expansion of C4 vegetation in their respective continents.
Despite the earlier innovation of C4 vegetation, the expansion occurred largely between 5-7 million years. Regions where it was delayed include Australia, parts of Asia (e.g., the Tibetan plateau), and large portions of Europe (where C4 grasses never became dominant, in large part due to occurring at higher latitudes that experience cooler climates). While we placed our data cutoff for inclusion during the Miocene to maximize the number of samples possible, we now do note the percentage of specimens that occur at during the early Miocene prior to the expansion of C4 grasses in their region. In regions where C4 expansion was delayed (e.g., Australasia, the Tibetan plateau), all serial samples occur during the Pliocene to late Pleistocene (well within the time frame where C4 plants had expanded). Further, in most of the studies from which data was gathered, the aim of serial sampling of tooth enamel was to infer the degree to which herbivores consumed C3 and/or C4 vegetation (with only a minority of studies conducted in primarily C3 ecosystems). We have clarified this in the methods section.

4. I think it would be worth mentioning the range of body masses of the sampled taxa before giving the body mass bins. Because the relationship between herbivore body size and dietary ecology is rather complicated, I think if an evaluation of the effect of body size is to be done, it needs to be done carefully. Brief justifications for how boundaries between the body size bins are drawn are necessary—as of now, 100 kg and 350 kg seem to be arbitrary. Ideally, the boundary values should be of some biological or physiological relevance. If that is the case, it needs to be explained. If the divisions are made primarily for statistical considerations (i.e. to have comparable numbers of individuals in small, medium, and large groups), this needs to be stated too.

   We used the body masses categories of Bunn 1982, Brain 1983, and commonly used by hundreds of others included Faith et al. 2019. We have clarified this in the methods section.

5. Even though the mean individual ranges are generally narrow, grazers’ range is ~1.6 times as wide as browsers’ (and 2.4 times for <37 deg latitude), and the ranges are also significantly different between browsers and grazers (Table 1). You should talk about what this range can mean, in terms of the vegetation consumed. This would be helpful to nonspecialist readers.

   We agree and have expanded the discussion of the δ^{13}C ranges of browsers and grazers, in terms of vegetation consumed.

Minor Comments:
Additionally, the paper would also use more consistent terminology, particularly when it comes to describing dietary groups. Some in-text references to figures are incorrect—not all figures cited show what the text is talking about. Figure captions and axis labels could also be more accurate and informative. The Introduction and Discussion sections will also need some rewriting. Detailed comments with references to line numbers:

37 “enamel” should be subscripted
   Done

39 maybe specify what you mean by dietary strategy by listing the three dietary groups in parentheses?
   Done. We have added what we mean by dietary strategy (i.e., browser, mixed-feeder, grazer).

40–43 the example of C. emsliei would probably go better with the previous sentence—that “almost all herbivores…are composed of individual specialists,” as it explains to readers clearly what you mean by individual specialists—than with the statement that this pattern holds true through time, as there is only one age associated with this example

   Great point, we have moved this up and now moved discussion of time to later in the abstract. We now state: “For example, Cormohipparion emsliei (Equidae) from the Pliocene of Florida (~5 Ma) exhibit a δ^{13}C_{enamel} range of 13.4‰, but all individuals sampled have δ^{13}C_{enamel} ranges of ≤2‰ (mean = 1.1‰). Most notably, this pattern holds globally and through time, with almost all herbivorous mammal individuals exhibiting narrow δ^{13}C_{enamel} ranges (≤3‰), demonstrating that individuals are specialized and less representative of their overall species dietary breadth.

54 “define”
   Corrected.

55 add “choice” after “habitat”, as diet does not directly influence the physical environment per se. The rest of the sentence also needs some re-writing for better clarity. For example, I would how animals move in their environment is equivalent to migration, while migration is one aspect of landscape use and should not be mixed up with the latter.

   Done. We have added choice after habitat, but have also clarified what we mean by “how animals move in their environment” as we literally mean how animals move (e.g., run, climb). We now state, “Diet influences an animal’s habitat choice, landscape use/migration, how animals move in their environment (i.e., their biomechanics as pertains to food acquisition), and even reproduction (1–4)”.

56 Before talking about humans, say a little more about how animals’ dietary niche, especially how niche breadths have typically been defined as either broad or narrow for a certain species, then transition into how this new niche is unique

   Done.

62 omit “for example”
   Done.
69–71 this sentence (“In fact…”) seems to imply that such investigations have been previously done many times and revealed robust patterns

*We removed “In fact” and added “—though only a handful of species have been examined.”*

76 thought to be or found to be?

*We removed this paragraph as suggested by this reviewer; no change is needed.*

79 move “dietary” to before “specialist” to make the sentence flow better

*Done.*

76–81 This paragraph seems redundant to me. Basically, it is saying with examples that some generalist species are composed of generalist individuals (thereby supporting the NVH) while many other species specialist individuals (thereby not supporting the NVH). Since this has already been stated in the previous paragraph, and carnivores are not the focus of this study, I recommend keeping only the last sentence of this paragraph.

*Done.*

97 before the term mixed-feeders appears here (for the first time), it is worth introducing your three dietary groups first and briefly explaining the conventional view of their dietary niche breadths

*Great point, we have now done this and the sentences read as follows: “Here, we use stable carbon isotope data from serial samples of mammal tooth enamel (δ\(^{13}\)C\(_{enamel}\)) collected from herbivores that can be categorized into the dietary groups of grazer, browser, and mixed feeder (i.e., eating both grass and browse). We gathered data from the literature dating from the Miocene to the present (298 individuals, 4013 samples) and acquired new samples of mixed-feeders (20 individuals, 121 samples).”*

102 the duration of tooth formation is relevant and important enough here that I think there is no need for parenthesis

*Parentheses were removed.*

109–113 I recommend removing the topics of “shifts in plant species composition” and “species distributions through time” from Introduction since you did not revisit these topics in Discussion

*Done.*

123 I cannot tell from Figs. 1–2 that there is as much as an 8‰ range in grazers. Only Fig. 3 shows that.

*Corrected.*

125–126 What’s in parenthesis here goes better after the first sentence of the paragraph where you report the total range of carbon isotope values. Also, is it necessary to list all the countries here? Perhaps it would be better to include a map of sample locations in the supplementary file.

*The full list is more extensive, these were just some examples; however, all countries are listed in the supplemental data table. We now clarify this and moved this statement to be a part of the first sentence, as suggested.*

134 “herbivores”

*Corrected.*

160 what sampling standardization?

*We have clarified this, by stating (i.e., the sliding window analysis).*

166–168 by “between” I think you mean “among”, since the comparisons involve more than three values

*Corrected.*

169 by “among” I think you mean “in”

*Corrected.*

176 again, Fig. 4 does not show individual variabilities, but averaged individual variabilities. The 8‰ range mentioned in this sentence is not shown in Fig. 4.

*Corrected.*

188–189 morphologically “and nutritionally” constrained; would also be good to include citations here about browsing species’ constraints

*Corrected.*

190–191 I’d be curious to see what their serial sample profiles look like, perhaps it would be worth graphing them (like what is done for C. emblie in Fig. 2) in the supplementary file.
This is a great suggestion, and we are happy to add this to the supplementary files (now Figure S3).

200–216 The argument in this paragraph is relatively weak. The fact that different parts of grass forage do not get selected upon as finely as the architectural heterogeneous browse materials would contribute to higher isotopic variability in grazers only if the different parts of grasses have highly variable isotopic signatures, and I’m not sure if that’s the case. I think how feeding selectivity translates to isotopic variability is a little more complex than what is described here.

Note that there is greater variability in the C3 plants than in C4 plants, and when grasses are consumed as a whole, only one overall isotopic signal is recorded in the teeth regardless of how much variability is among the plant parts. Additionally, the second sentence (tradeoffs for consuming grasses) and the last sentence (mixed feeders having the lowest III indices) of this paragraph seem out of place. Their logical linkage to the rest of the paragraph is not strong. You need to write elaborate on both statements if you keep them where they are.

We have reorganized and largely rewritten this paragraph to make the following points: 1) $\delta^{13}C_{enamel}$ values can vary spatially based on habitat heterogeneity and selection of plant parts by herbivores, 2) the high variability in grazers, while potentially stemming from spatial variability is unlikely stemming from isotopic variability within grasses, due to challenges of foraging on discreet plant parts with different isotopic values.

217–218 While time averaging does not affect what you found for individual teeth (Figs.1-3), you may want to consider how it may affect your calculated III indices (Fig. 4). In other words, the III values of extinct taxa are potentially lowered by the effect of time averaging.

We have now included discussion of how III indices pertain to extant vs. extinct taxa.

223 this “example” does not match what you just talked about…it is critical in this paper to address the dampening effect of recorded isotopic signatures, and to make a sound argument here you need examples of a single tooth recording a wide range of carbon isotope values

We have changed the example here to instead focus on the fact that a single tooth can have high variability; thus, while it is possible, it is just rare. See discussion.

226 I am a little bothered by “there is no reason why…”, as you are trying to give an example to support an argument. The absence of evidence is not the evidence of absence.

This has been removed, as a different example is used to support the statements in the paragraph.

227–228 Sentence in parenthesis is a little redundant

This has been removed, as a different example is used to support the statements in the paragraph.

239 what roles?

We have now stated, “Individual foraging behavior can determine how other members of a foraging group behave, a group’s choice of where to forage, and foraging methods and their successes (48–51), while individual temperament can affect predator-prey interactions (52).”

243–247 These two sentences are a bit confusing. First, you talk about individuals consuming disparate foods, which to me implies more generalist individuals, then you talk about individual specialization in the second sentence. Perhaps you can modify the phrasing in the first sentence.

We have modified the phrasing in the first sentence.

251 what do you mean by “extreme”? is there a reason to emphasize on extreme generalists (as opposed to other, less extreme generalists) here?

We have removed the word extreme as it doesn’t change the meaning of our sentence. Good point!

277 Fig. 4 does not indicate age, nor are taxon ages noted in the supplement

We have reworded this statement.

Comments on figures and tables:
In all figures the Y-axis label should include “enamel” to match the text, and the unit should be in parenthesis, making it: $\delta^{13}C_{enamel}$ (‰)

Corrected.

Figure 1
554 “breadths”

Corrected

555 “if individuals have more specialized (left) or more generalized (right) diets”
This figure is very intriguing and informative, with theoretical predictions (left and middle columns) and empirical results (right column) shown simultaneously. It is probably the one figure that best summarizes the key findings of this study, and so it would be good to improve it further. I have three suggestions: (1) Symbols in figure legend should match the colors in the graph, since each symbol (species) only has one corresponding dietary assignment (color). (2) In the figure caption, it would be worth noting that tooth crown height generally increases with higher levels of grazing. (3) It is not clear to me why these six taxa are chosen as examples to be presented here. Why not illustrate the entirety of your dataset?

We have only provided a subset of these data to illustrate these points (as examples), due to the need for visual clarity. If we had plotted all data, it would not be possible to make sense of any of these data. Please note that we summarize all data in Fig 3 and in all subsequent analyses. Further, we have also added examples with the highest variability to Figure S3.

Figure 2

563 “(range = 13.4‰)”
Corrected

564–565 just say “browsers” and “grazers” since (1) “obligate” is not defined or used elsewhere in the paper, and (2) in the literature, obligate grazers are distinguished from variable grazers and have quantifiable defining criteria, so do not mix up grazers with obligate grazers if what you really mean here is grazers

We have removed the word obligate here so as not to confuse the reader. Thanks!

Figure 3

569–570 end members of a range should have the same number of decimal places
Corrected

570 not clear to me what you mean by “methods”
For each panel, give the sample size (numbers of individuals) of the dataset (n = #). Avoid using “trophic group” in Y-axis labels, since you don’t use these words anywhere else in the paper. Just say “dietary category.” I would also remove “Individual Isotopic Variability” from the panel headings, since they are all the same, and incorporate the phrase into figure caption if necessary.

We have changed this to, “when calculated using the full range of statistical methods.”

Figure 4

Panels A) and C) need more informative Y-axis labels (add “species” to Y axis to contrast the “average individual” on X axis)
I don’t really see what you describe about panel C)—that species in low latitudes plot close to the 1:1 line than other species.
Figure caption should include explanation for the box and whisker plots; alternatively, add an inset diagram to panel B) or D).

We have made this change to panels A and C.

Table 1
To my understanding, “n” denotes number of individuals for range (top half of the table) and number of species for III (bottom half of the table). If so, the abbreviation explanation should be corrected at the bottom of the table.
Corrected

Reviewer #2: This manuscript analyzes a dataset of stable carbon isotope serial samples from mammalian herbivore dentitions to ask whether ‘dietary generalism’ in a species emerges from intra- or inter- individual dietary variation. They find that most generalist species are comprised of individual specialists, with grazers showing the highest levels of individual variation (based on the authors’ isotopic individuality index).

This is an interesting ecological question, but it has been addressed in previous work as noted in the introduction. Nonetheless, this study’s synthesis of existing stable isotope data in the literature and inclusion of new samples from C3-C4 mixed-feeding taxa is a nice addition to the existing literature. I have a few comments/questions for the authors to consider.

We thank the reviewer and do want to make clear in this paper that we are building off the work and ideas of others and have tried to make this clearer in the discussion and conclusion, adding in reference to those earlier cited papers in the discussion.

Major Comments
Isotopes are a proxy for diet and record dietary information over specific time scales. There is surprisingly no discussion of how dental maturation rates across taxa relate to serial samples, given the fact that sampling rates and distances vary, in addition to fundamental differences in the dental biology of taxa analyzed. The authors consider variation in crown height (and use a five-sample sliding window in an attempt to control for this) but should also discuss how variation in the timing of the individual’s life is reflected in serial samples—Are all samples considered to be annual, semi-annual? Does this vary across taxa? Does it matter? Without these considerations, the manuscript feels incomplete.

I ask these questions because depending on the scale of diet information recorded, you could have a scenario where a dietary generalist looks like a specialist (from the view of isotopes) because of temporal averaging of isotope signals. We all acknowledge that bulk samples record average diet, but even serial samples are averaging diet over a certain span of time. If that span of time
systematically varies across taxa, that adds a major complication. For example, could greater intratooth d13C range in grazers reflect faster dental maturation times due to taller crowns and thus less temporal averaging of isotopic variability?

We thank the reviewer for pointing out these omissions. As most of these studies were done with the aim of being largely comparable to one another, the effect of temporal averaging is fairly similar across taxa. That being said, discussion of this has been added to the discussion section.

How does consideration of variation in plant isotopic composition impact these conclusions? For example, Cerling and others have discussed differences between NADP and NAD+PEP-CK grasses in the African context. Could systematic differences in isotopic variability between browse and graze impact your findings?

We don’t believe differences in NADP and NAD+PEP-CK grasses would contribute significant variability in grasses, as the difference between these sub-pathways is only ~1‰. We now cite their work and mention this in the discussion.

Minor Comments

pg 7, line 217-220: But what about time in terms of the osteological collections? A lot of museums house collections that were collected across several decades, if not centuries, and probably sample sporadically across a species’ geographic distribution. Could species dietary niches shift on those scales?

While it is possible for animals to switch diets over a period of years to decades, each analysis is focused on the duration of time during which a tooth is mineralized, so ~1 year. We don’t discount this possibility for longer term change and have added discussion of this to the discussion.

pg 9, line 382: “Individuals identified to the genus level were lumped with congener individuals identified to the species level when it could be reasonably inferred that they belonged to the same species (e.g., Mammuthus sp. lumped with Mammuthus columbi)” –does this vary by feeding group? Could unidentified species be inflating genus level variation?

We changed this to: “We only analyzed those teeth with at least five serial samples. Individuals identified to the genus level were lumped with congener individuals identified to the species level only when it could be reasonably inferred based on location and geological time period that they belonged to the same species (i.e., Mammuthus sp. lumped with Mammuthus columbi).” We only did this for Mammuthus based on expert consensus that this is the case.

Summary

Collectively, this manuscript has been well reviewed by all reviewers and we were able to address all of the reviewer comments and suggestions in the resulting manuscript. Included is a track-changed version of the manuscript. The manuscript contains four color figures and supplementary information (we have added one supplemental figure, based on feedback from Reviewer 1). The corresponding author’s contact information for communication regarding this manuscript is stated above (e-mail: larisa.desantis@vanderbilt.edu).

Thank you for your continued consideration of the manuscript.

Sincerely,

Larisa R. G. DeSantis and co-authors
Global long-term stability of individual dietary specialization in herbivorous mammals

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Classification

Biological Sciences: Ecology; Physical Sciences: Earth, Atmospheric, and Planetary Sciences

Keywords

carbon isotopes, diet, generalist, serial samples, specialist

Author Contributions

L.R.G.D. and M.A.G. conceptualized the project, M.I.P., M.A.G., and L.T.Y. compiled published data with assistance from L.R.G.D., L.R.G.D. and L.T.Y. generated new data, M.I.P. and A.D. performed statistical analysis, R.C.H. provided access to and contextual information pertaining to newly sampled specimens, L.R.G.D., M.I.P., and J.L. wrote the manuscript with contributions from A.D., M.I.P. made the figures, all authors contributed edits and intellectual contributions.

This PDF file includes:

Main Text
Figures 1 to 4
Tables 1 to 2
Abstract

Dietary variation within species has important ecological and evolutionary implications. While theoreticians have debated the consequences of trait variance (including dietary specialization), empirical studies have yet to examine intraspecific dietary variability across the globe and through time. Here, we use new and published serial sampled δ\textsuperscript{13}C\textsubscript{enamel} values of herbivorous mammals from the Miocene to the present (318 individuals summarized, 4134 samples) to examine how dietary strategy (i.e., browser, mixed-feeder, grazer) affects individual isotopic variation. We find that almost all herbivores, regardless of dietary strategy, are composed of individual specialists. This finding holds through time: for example, Cormohipparion emsliei (Equidae) from the Pliocene of Florida (~5 Ma) exhibit a δ\textsuperscript{13}C\textsubscript{enamel} range of 13.4‰, but all individuals sampled have δ\textsuperscript{13}C\textsubscript{enamel} ranges of ≤2‰ (mean = 1.1‰). Most notably, this pattern holds globally and through time, with almost all herbivorous mammal individuals exhibiting narrow δ\textsuperscript{13}C\textsubscript{enamel} ranges (≤3‰), demonstrating that individuals are specialized and less representative of their overall species dietary breadth. Individual specialization likely reduces intraspecific competition, increases carrying capacities, and may have stabilizing effects on species and communities over time. Individual specialization among species with both narrow and broad dietary niches is common over space and time—a phenomenon not previously well recognized or documented empirically.
Food selection is a critical component of life at the individual, population, and species level, and is one of the crucial aspects that defines the ecological niche of an organism. Diet influences an animal's habitat choice, landscape use/migration, how animals move in their environment (i.e., their biomechanics as pertains to food acquisition), landscape use/migration, and even reproduction (1–4). The dietary niche of an animal is often then inferred as broad (i.e., a generalist) or narrow (i.e., a specialist) based on the breadth of food items consumed. Humans are no exception, with the genus Homo having recently been credited as occupying a previously empty niche—that of a ‘generalist specialist’, defined as the ability to both generalize (as a species) and specialize (as individuals) in one's environment (5). While Homo sapiens are highly generalized in their dietary behavior and individually maintain specialized diets through time, the ‘generalist specialist’ niche may be far more widespread than our species.

The Niche Variation Hypothesis (NVH), for example, suggests that populations of species with broader niches are also more variable in a particular trait (e.g., morphological, physiological, behavioral) than more specialized populations (6). Increased niche breadth by a species could result either from individuals expanding their use of available resources, or individual specialists maintaining narrow diets but collectively resulting in a broad species niche (7, 8). While empirical tests typically fail to support the NVH, the absence of confirmation has largely been attributed to the use of morphological traits (e.g., beak size or shape) as proxies of dietary breadth, in contrast to more direct measures of diet (8). In fact, when diet is examined directly or inferred via proxies such as stable isotopes, generalist populations/species are often found to be composed of individual specialists (8–12)—though only a handful of species have been examined (8–12). The reason for this phenomenon is not entirely clear, but for carnivores at least, it is likely related to tradeoffs between specializing on one versus many prey species, with selection acting against individual generalists (7). For example, pursuing voles, rabbits, and deer may make an individual predator less effective at capturing any one of these prey items, resulting in a ‘jack of all trades and master of none’ outcome.

Gray wolves and tiger sharks are thought to be true generalists, both at the individual and species level (9, 13). On the other hand, carnivores such as loggerhead turtles, Brünnich's guillemot, sea otters, and bull sharks show less intra-individual dietary variation than inter-individual variation, revealing the presence of individual specialists within more dietary generalized populations or species (9–12). While this phenomenon has been relatively well studied in carnivores (9–13), herbivorous generalists have received less attention in comparison.

Food selection in herbivores results from the complex interplay between vegetation characteristics and herbivore anatomy, physiology, and behavior, a series of ecological and evolutionary interactions that occur at the species, population, and individual levels (14). Herbivore food selection is often a balancing act between the quality of digestible dry matter (energy and macronutrients) in each bite (15) and chemical defenses such as phenolics, terpenes, and toxins (16, 17). Individuals experience tradeoffs related to search time, nutrient content, and other fitness tradeoffs (e.g., optimal foraging theory; (18–21)). Plant selection is further dictated by herbivore body size, through characteristics such as bite size and length of the digestive tract (17, 22). While foraging behavior is relatively well studied in modern systems, few empirical studies have examined dietary variability in extant or extinct herbivores, or addressed how food selection at the individual level scales up to the species level. That is, are generalist species composed of similarly generalized individuals or specialized individuals subdividing the species’ dietary niche axis? How general is either pattern over time?

Here, we use stable carbon isotope data from serial samples of mammal tooth enamel ($\delta^{13}C_{\text{enamel}}$) collected from herbivores that can be categorized into the dietary groups of grazer, browser, and mixed feeder (i.e., eating both grass and browse). We the gathered data from the literature dating from the Miocene to the present (298 individuals, 4013 samples), and acquired
new samples of mixed-feeders (i.e., eating both grass and browse; 20 individuals, 121 samples). Enamel δ\(^{13}\)C values provide valuable insights into herbivore ecology, including a record of the proportions of C\(_3\) and C\(_4\) vegetation consumed, indicative of trees/shrubs and warm-season grasses, respectively—when occurring at lower latitude sites (~37° and below; (23–25)). Because teeth grow incrementally, serial samples of enamel collected perpendicular to a tooth’s growth axis can record dietary variability over the course of the tooth’s growth (which can range from a few months to over two years in high-crowned teeth; (26, 27)). As a result, our new dataset allows us to answer the following questions: (1) are herbivorous generalists (i.e., mixed-feeders) composed of individual generalists (defined as having high isotopic variation) or individual specialists (defined as having low isotopic variation) (Fig. 1); and, (2) how do isotope values of individuals vary within a species’ overall dietary strategy (i.e., browser, mixed-feeder, grazer)? These answers provide a long-term view of herbivore-vegetation interactions critical for understanding intra- and inter-specific competition and their ecological and evolutionary consequences, shifts in plant species composition, and species distributions through time (23, 28). Understanding how herbivores choose and consume vegetation at the individual, population, and species levels is also fundamental for effective environmental conservation and management (29), especially during the Anthropocene (30, 31).

Results
Review of the literature and stable isotope sampling of mixed-feeders resulted in 4134 serial samples from 318 individuals (Supplemental Dataset). Descriptive statistics of δ\(^{13}\)C enamel values are noted for these samples in Tables 1-2, Supplemental Tables 1-9, and summarized in Figs. 1-4 and Figs. S1-S2S3.

Mammalian herbivore δ\(^{13}\)C\(_{\text{enamel}}\) values spanned 23‰ (ranging from -20.3‰ to 2.7‰) across all individuals, which includes specimens from grasslands to rainforests across the globe (e.g., Afghanistan, China, Ethiopia, Ireland, Panama, South Africa, USA; see Supplemental Dataset for a full list of the countries included). The δ\(^{13}\)C\(_{\text{enamel}}\) range within a given species can be upwards of 8‰ in grazers (Fig. 1-3), or approximately 35% of the total range represented in this study (which includes grasslands to rainforests across the globe, e.g., Afghanistan, Bulgaria, Chad, China, Ethiopia, Ireland, Jordan, Mexico, Pakistan, Panama, Scotland, South Africa, Ukraine, USA). In contrast, the range within each individual specimen is low (typically less than 3‰; Fig. 3). For example, the total species range of the mixed-feeder Cormohipparion emsliei from the early Pliocene (Florida, USA; (32, 33)) is 13.4‰, while individuals have an average δ\(^{13}\)C\(_{\text{enamel}}\) range of 1.1‰ (standard deviation, SD 0.5‰, n = 9; Fig. 2), and all individuals vary by ≤ 2‰. An additional mixed feeder targeted for sample collection (Hemiauchenia macrocephala) also demonstrates a broad δ\(^{13}\)C\(_{\text{enamel}}\) range of 13.2‰ from two sites in Florida (Inglis 1A and Leisey 1A; (34)), with an average individual δ\(^{13}\)C\(_{\text{enamel}}\) range of 1.3‰ (SD of 0.5‰, n = 8), and all individuals exhibit ≤ 2.4‰ variability (Fig. 1). All individual generalist herbivorous herbivores (i.e., mixed-feeders) have δ\(^{13}\)C\(_{\text{enamel}}\) ranges ≤ 4.0‰ with average individual δ\(^{13}\)C\(_{\text{enamel}}\) ranges of < 2‰.

Nearly all herbivorous mammalian individuals are specialized in their diets (Fig. 3). Specifically, the majority of individuals sampled with at least three serial samples (89%, 283 of 318 individuals) or five or more serial samples (87.9%, 246 of 280 individuals) exhibit a δ\(^{13}\)C\(_{\text{enamel}}\) range ≤ 3‰ (Fig. 3). As body size is known to influence diet, including an animal’s ability to eat lower quality and foliage like grass (35), relationships between individual breadth in δ\(^{13}\)C\(_{\text{enamel}}\) and body size were examined. Specifically, we tested for significant differences in the total range of δ\(^{13}\)C\(_{\text{enamel}}\) values of small (mass <100 kg), medium (100 kg ≤ mass <350 kg), and large (mass ≥350 kg) species, as well as the average range exhibited by individuals across these size categories. We also reran our analyses on only specimens found below 37° latitude, where the isotopic distinction between grasses (primarily C\(_4\)) and trees/shrubs (primarily C\(_3\)) is clearest (23–...
There are no significant relationships between average individual ranges or of average taxon $\delta^{13}C_{enamel}$ ranges across body size categories, either globally or at low latitudes (Table S6), contrary to expectations (36). However, when data were corrected with a sliding window (due to the possibility that more serial samples could produce larger $\delta^{13}C_{enamel}$ ranges; see Materials and Methods), the average individual range of large taxa is significantly greater than medium-sized taxa ($p<0.05$), but not small taxa ($p>0.42$; Table S6).

The Isotopic Individuality Index (III) for a given species, as defined here, is the ratio of the average individual $\delta^{13}C_{enamel}$ range to the total $\delta^{13}C_{enamel}$ range of a species. This proportion is low (near 0) when individuals are specialized within isotopically generalized species; the III approaches 1 when an individuals’ isotopic breadth approaches the overall species breadth (Fig. 4). The average Ills calculated for mixed-feeding species (0.18±0.11, $n=4$), browsers (0.35±0.17, $n=7$), and grazers (0.39±0.17, $n=10$) are all closer to 0 than 1, with only grazers having significantly higher III values than mixed-feeders when including the global dataset ($p<0.05$) (Fig. 4; Table 1, S7). Below 37° latitude, the III of grazers is significantly higher than both mixed-feeders ($p<0.05$) and browsers ($p<0.05$). It should be noted that sampling standardization (i.e., the sliding window analysis) of the global dataset results in significantly lower III values in mixed-feeders as compared to browsers, $p<0.01$ (Tables S8, S9). Variance partitioning analyses (where the proportion of $\delta^{13}C_{enamel}$ variance is partitioned across three nested scales: between species, between individuals, and within individuals)(37) similarly found that, across dietary groups, individuals within species tend to be specialized (Table 2). Lower variance is consistently found within individuals as opposed to between among individuals in a species, or across species: depending on the specific analysis used, the proportion of variance ranges from 0.34-0.64 between species, 0.32-0.61 between individuals within a species, and 0.05-0.06 between serial samples within individuals (Table 2).

Across the global data set, the average individual $\delta^{13}C_{enamel}$ range is highest among grazers, significantly higher than browsers (Table 1). Below 37° latitude, the average individual $\delta^{13}C_{enamel}$ range remains highest among grazers and is significantly higher than both browsers and mixed-feeders (Table 1). All dietary categories have mean $\delta^{13}C_{enamel}$ ranges of $<3\%\text{o}$, grazers yielded a maximum individual range of $8\%\text{o}$, while the individual $\delta^{13}C_{enamel}$ ranges of browsers and mixed-feeders in the dataset never exceeded $3.3\%\text{o}$ and $3.9\%\text{o}$, respectively (Fig. 3 and 4). When we standardize the number of analyzed serial samples per tooth using a five-sample sliding window approach (see Materials and Methods), we find similar results to the raw data analysis (Fig. S1, Table S5). Most individual ranges (92-94%) are $\leq2\%\text{o}$ when standardized, and nearly all (97-100%) are $\leq3\%\text{o}$ across dietary groups (i.e., global average; Fig. S1, Table S5).

Discussion

Effects of dietary behavior on individual specialization

Herbivores that are classified as grazers vary their diet the most individually, more so than herbivores classified as browsers and mixed-feeders. Some of the largest individual $\delta^{13}C_{enamel}$ ranges are exhibited by grazers (e.g., bison, horses, mammoths, and wombats can exhibit individual $\delta^{13}C_{enamel}$ ranges of 6.7‰, 6.7‰, 7.6‰, and 8.0‰, respectively; Fig. S3); however, their mean is still fairly constrained ($\bar{\epsilon}=1.8\%\text{o} \pm 1.5$ SD). As grazing morphologies permit, but do not exclusively prescribe, grass consumption (38), dietary variability of individuals is likely to be broader when a given taxon is capable of eating grass and/or as well as a mixed-feeding diet. Browsing species are morphologically and nutritionally constrained to diets that exclude grasses (39), and exhibit the lowest $\delta^{13}C_{enamel}$ ranges (Fig. 3, Table 1), which could explain the broader $\delta^{13}C_{enamel}$ ranges of grazers as compared to browsers (~1.6 to 2.4 times that of browsers; Table 1). Some of the largest individual $\delta^{13}C_{enamel}$-ranges are exhibited by grazers (e.g., bison, horses, mammoths, and wombats can exhibit individual $\delta^{13}C_{enamel}$ ranges of 6.7‰, 6.7‰, 7.6‰, and
While many large herbivores are grazers, and body size of the individual also impacts the plant types, parts, and volume that can be ingested (36, 39), a range of body sizes are represented in each dietary category. Further, our results suggest that body size, alone, is not significantly influencing individual specialization. It should be noted that while small herbivores were analyzed (<100 kg), the smallest mammals (<10 kg; e.g., most rodents) are not included in this analysis due to the size required for serial sampling of individual teeth. While more work is needed on small mammals, modern mark re-capture studies suggests that small mammals can also be individually specialized (40).

The fundamental differences between grass and browse resources are exploited by herbivores can affect $\delta^{13}$C$_{enamel}$ ranges among grazer and browser may also account for greater individual $\delta^{13}$C$_{enamel}$ ranges among grazer species. Specifically, mammalian herbivores broadly record $\delta^{13}$C$_{enamel}$ variability of plants on the landscape; depending on the size of their home range, this could introduce spatial variability in $\delta^{13}$C$_{enamel}$ that may be expected to increase with body size (and inferred home range size). While many large herbivores are classified as grazers, and body size of the individual also impacts the plant types, parts, and volume that can be ingested (36, 39), a range of body sizes are represented in each dietary category. Further, our results suggest that body size, alone, is not significantly influencing individual specialization. It should be noted that while small herbivores were analyzed (<100 kg), the smallest mammals (<10 kg; e.g., most rodents) are not included in this analysis due to the size required for serial sampling of individual teeth. While more work is needed on small mammals, modern mark re-capture studies suggests that small mammals can also be individually specialized (40).

Fundamental physiological differences between grasses and browse, and their distribution across the landscape, may influence spatial heterogeneity and variation in the $\delta^{13}$C$_{enamel}$ values recorded in herbivore enamel. Grasses typically exhibit fewer secondary plant chemicals such as tannins and alkaloids and that can change more seasonally than leaves and buds (17), contributing few tradeoffs for their consumption if herbivores can compensate for their typically lower nutritional content and abrasive nature (i.e., presence of phytoliths which can wear down teeth (41)). C$_4$ grasses that are more arid adapted and utilize the PEP-CK sub-pathway can also have more negative values than grasses that use the classic NADP sub-pathway, though differences are small (~1‰) (42). From an ungulate perspective, the architectural arrangement of grass means that it cannot be as easily differentiated via dietary selection as can browse—grasses are composed of leaves, sheaths and fruit that differ only at the very fine scale, they have a low growth form, and grow in continuous dispersion on the landscape (17), making it less likely that individual grazers (typically with broad muzzles) can more finely select grass forage. In contrast, browse consists of a heterogeneous mix of leaves, buds, and woody stems that are irregularly distributed over the topology of the plant, and are discretely dispersed (17). Thus, active food selection by of browse resources browsers and mixed-feeders can lead to narrower dietary niches in browsing and mixed-feeding taxa these taxa (39) but is unlikely to be the source of higher $\delta^{13}$C$_{enamel}$ variation in species consuming primarily grasses. This is somewhat reflected in our data by the higher individuality indices (i.e., the $\delta^{13}$C$_{enamel}$ $\delta^{13}$C$_{grains}$ of individuals are closer to the total $\delta^{13}$C$_{grains}$ ranges of a given species) across-of taxa classified as grazers, though browsers have similar III values to grazers as compared to other dietary groups likely stems from their ability to eat diverse food types in addition to grasses (with few consequences).

Mixed-feeders, despite eating the broadest mix of food types, have the lowest III indices (significantly less than grazers; Table 1). While we would expect lower III indices for mixed-feeders if individuals variation is comparable to y as much as grazers or browsers, due to the overall larger breadth represented by themixed-feeding species. However—nevertheless, individual specialization of mixed--feeders is far below that represented by the species and does
not indicate examples of switching between the consumption of primarily grass at one interval to the consumption of primarily browse as another. Lastly, while III indices of fossil taxa could be lower than extant taxa due to time averaging that contributes to species breadth calculations (i.e., the denominator of the III values), the vast majority of all specimens included (~96%) are from fossil specimens and are relatively comparable to one another (Supplemental Dataset SD1).

While time averaging could cause $\delta^{13}C$ ranges of extinct species to appear broader than they may have been during a particular moment in time, it is compelling that the vast majority of mammals exhibit narrow isotopic variability for comparable durations (months/seasons) of an individual's life (Fig. 3, Table 1). We can't discount the possibility that herbivores change their diet later in life or over the course of years to decades; however, serial sampling of multiple teeth per individual (i.e., spanning years, though not decades) reveals the absence of significant dietary variability in the majority of specimens (though this has only been documented in a handful of studies (43-45)). Further, although stable isotopes in teeth are known to be dampened compared to the isotopic composition of diet or water consumed (26, 4246, 4347), a given mammal tooth has the potential to reflect the full isotopic range of a given species (e.g., have $\delta^{13}C_{enamel}$ values that range from -40.9‰ to 0.14‰). For example, bison, horses, mammoths, and wombats (all grazers) can exhibit individual $\delta^{13}C_{enamel}$ ranges of 6.7‰, 6.7‰, 7.6‰, and 8.0‰, respectively (Fig. S3) demonstrating that even when isotopes are dampened high-variability is rare but possible. That being said, serial samples represent an averaged diet over the period of time sampled and do not represent the full isotopic range of plants consumed by the individual during this period of time, especially if mixed feeders are consistently consuming the same proportions of mixed vegetation. While the total $\delta^{13}C_{enamel}$ range from an individual tooth is only a minimum estimate of total plant isotopic variability (due to the signal attenuation of enamel as compared to plants consumed by the herbivore) it does provide important insight into dietary variability of individuals (and is a useful tool for comparing taxa with different dietary preferences as dampening is likely to effect herbivorous mammals to a similar degree. Individual teeth from C. emsli (32, 33) have a total $\delta^{13}C_{enamel}$ range of 13.4‰, in stark contrast to individuals which average 1.1‰ (and all have ≤ 2‰ variability in $\delta^{13}C$ values). While the isotopic range of plant values may be far greater than 13.4‰, there is no reason why individual specimens of C. emsli cannot vary as much as 13.4‰ (i.e., we are comparing $\delta^{13}C_{enamel}$ variability of a given individual to the $\delta^{13}C_{enamel}$ variability of a species). Other mixed-feeders with broad isotopic ranges (e.g., Hemiauchenia macrocephala, Platynous vetus, and Diprotodon optatum (34, 4448)) individually exhibit only a fraction of the isotopic variability of a given taxon (Fig. 4). Most notably, very few individuals (1.2%) exhibit a broad isotopic range (i.e., individual $\delta^{13}C_{enamel}$ range > 7‰), demonstrating both the possibility of high $\delta^{13}C$ variability in an individual, but also the rarity of such occurrences.

Dietary specialists across space and time

Our results suggest that herbivorous mammals are primarily individual specialists regardless of dietary category. similar to observations noted for carnivorous taxa (9-13). The individual variation we observe in herbivorous mammals across the globe and through time have important ecological and evolutionary implications (8, 28, 4549, 4650). Fundamentally, trait variation among individuals is the raw material natural selection acts upon (4751). Individual foraging behavior can determine roles-in-a-how other members of a foraging group behave, a group’s choice of where to forage, and foraging methods and their successes (48-5152-55), while individual temperament can affect predator-prey interactions (5256). An animal's temperament and the individual dietary choices it makes (including high-degrees of individual dietary specialization) are often associated with ecological interactions that promote food web stability in diverse communities (5256).
among and between species (niche complementarity) \((\text{5559})\). Alternatively, trait heterogeneity may be a consequence of a release of intraspecific competition resulting in increased niche widths in populations that are decoupled from individual niche width \((\text{5660})\).

Generalist herbivore species are mostly composed of individual specialists and not individual generalists (Fig. 1). If extreme generalists were composed of individual generalists, one might expect fitness tradeoffs with the ‘jack of all trades but master of none’ strategy. Analogously, foraging behavior among herbivores may have similar tradeoffs pertaining to an individual animal’s ability to search for and digest disparate food types \((\text{5761})\). Generalist populations or species composed of individual specialists may have overall increased resilience against extinction if vegetation, patch size, and conditions affecting foraging behavior change dramatically over time. Notably, species with a high heterogeneity of dietary behavior and/or other functional traits have a higher probability of persisting as environmental conditions change—having a stabilizing effect that may result in increased species longevity \((\text{28, 5862})\).

Strict-sense species selection is defined as a clade-level relationship between species diversification rate and some emergent species-level trait that cannot be scaled down to the organismic level \((\text{5963, 6064})\)), but empirical support for this has been controversial. Our results show, at least in mammalian herbivores, that being a dietary generalist at the species level is decoupled from the organismic level, where individuals are for the most part dietary specialists. These results add to prior work, including on more carnivorous species that also provide support for this phenomenon \((\text{8-13})\). Therefore, if species-level dietary generalization/specialization is shown to vary with species diversification rates \((\text{e.g., } (6165))\), this would provide empirical support for strict-sense species selection in mammalian herbivores. These observations would have important conservation implications, as species survival for threatened herbivores may hinge on managing populations and landscapes in ways that place dietary specialized individuals in different habitats in order to preserve species-level generalization—an urgent mandate, given the existential threats facing many mammalian herbivores around the world \((\text{6266})\).

Herbivores select food in a hierarchical fashion, with individuals and populations making decisions at different spatial scales. At the individual level this relates to the size of the bite and the plant part exploited, and extends to the landscape and regional scale for populations \((\text{17, 39})\). Our data extends this spatial perspective through time to include specimens from the Miocene to the Present. Individual foraging decisions in herbivores are largely consistent through the time of tooth mineralization but are not representative of the realized niche of the species \((\text{Fig. 4})\). This suggests that individual temperament and/or learned behavior may have contributed to the way herbivores exploit plants throughout the geological record, and that ecological processes similar to those at play today \((\text{e.g., intra specific competition, tradeoffs in resource exploitation})\) have fostered individual specialization within generalist species through millions of years, a pattern with profound evolutionary implications. Across time and space, generalist herbivore populations are not “jacks of all trades and masters of none”; because each individual “jack” specializes in a dietary “trade,” populations can become “jacks of all trades and masters of all.” Individual specialization is not limited to generalist species but instead occurs in the vast majority of extant and extinct mammals examined here, suggesting there is a selective benefit of individual specialization. Far from being a characteristic unique to \textit{Homo sapiens}, the ‘generalist specialist’ niche can be viewed as a ubiquitous characteristic of generalists that may help promote the stability of complex and diverse communities and have the potential to contribute to species longevity.

\section*{Materials and Methods}

\textit{Stable Isotope Analyses}—Published data were obtained through a literature search of the topics of “isotop* AND fossil” or “isotop* AND tooth” through Web of Science. Publications with serial sample data \((\delta^{13}\text{C}_{\text{enamel}} \text{ from the carbonate portion of tooth enamel hydroxyapatite})\) from mammal
teeth around the globe and across the Neogene were curated in a database (Supplemental Dataset SD1, referred to as the ISOSERIAL 1.1 database). The identity of the sample (including the published taxonomy along with any revisions), measured $\delta^{13}C_{\text{enamel}}$ values, the distance each sample was taken along the growth axis of the tooth, and the publication reference were recorded, when available. Additional metadata, including the museum collection ID and specimen number, the absolute or relative age of the specimen, and location data (name, country, and state of the site the specimen originated from) were collected. Some publications only reported summary statistics from the isotope values for a given study (e.g., min, max, mean, standard deviation, range); these were recorded and indicated separately, along with their corresponding metadata (SD1). Domesticated and zoo specimens, marine mammals, and xenarthrans were excluded from data collection (the latter which lacks tooth enamel). A total of 3330 raw serial samples are included in the database with summary values recorded for 332 individuals (4134 serial samples), including 121 new stable isotope serial samples from 20 individual mixed-feeders (Table S1-S3, Supplemental Dataset SD1, ISOSERIAL 1.1 database).

The focus of this dataset is medium- to large-sized herbivores (i.e., ungulates and proboscidians). The majority of all data included in this database are from herbivores that occur during or after the expansion of C$_4$ grasses in their region, with only ~7% of data occurring in low-latitude regions prior to the expansion of C$_4$ grasses, in the early-middle Miocene (based on Ref. (23)).

Of the new data collected for this publication, mixed-feeding taxa were targeted for serial sample analysis as they were rare in published literature and are of particular relevance to the research questions. All newly sampled specimens are noted in Table S1-S3, Supplementary Dataset SD1, and are housed in publicly accessible collections in the Florida Museum of Natural History (Gainesville, FL, USA). Approximately 1-2 mgs of enamel powder were drilled perpendicular to the growth axis of the tooth, using carbide drill bits and a variable speed rotary style tool. The spacing of the samples varied and is indicated in Supplementary Dataset SD1 and Table S2. Enamel powder was treated with 30% hydrogen peroxide to remove organic material, rinsed, reacted with 0.1 N acetic acid to remove diagenetic carbonates (6367), and rinsed again after 18 hours (per (34)). The treated and dried enamel powder was analyzed using a VG Prism stable isotope ratio mass spectrometer with an in-line ISOCARB automatic sampler in the Department of Geological Sciences at the University of Florida. The analytical precision is ± 0.1‰, based on replicate analyses of samples and standards (NBS-19). Stable isotope data are reported in conventional delta ($\delta$) notation for carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$), where $\delta^{13}C$ (parts per mil, ‰) = ($R_{\text{sample}}/R_{\text{standard}}$)-1)*1000, and $R^{13}C/^{12}C$; $\delta^{18}O$ (parts per mil, ‰) = ($R_{\text{sample}}/R_{\text{standard}}$)-1)*1000, and $R=^{18}O/^{16}O$; and the standard is VPDB (Pee Dee Belemnite, Vienna Convention) (6468). All stable carbon isotopes are from the carbonate portion of tooth enamel hydroxylapatite.

Dietary classification—Each taxon was categorized as a browser, grazer, or mixed-feeder according to literature consensus. For extant species, this was determined by the observed diet of wild caught specimens (note, only wild caught specimens were included in the database; hence, no domesticated species were included from modern or archeological sites). For extinct species, these determinations were made based on studies of analogous morphology with living species. Taxon names, diets, and the references used to justify the assignments for extinct taxa are given in Table S10.

Statistical analyses—The minimum, maximum, range, mean, and standard deviation of the measured $\delta^{13}C_{\text{enamel}}$ Serial samples were calculated for each individual included in the database (Supplementary Dataset S1). When multiple publications reported data from the same specimen, values from the earliest publication were used and referenced. When serial samples were from multiple teeth from the same individual, summary statistics were calculated from the combined serial samples of the individual. Individuals were analyzed if they had at least three serial samples for a given tooth.
To explore whether diet type influences individual δ13Cenamel breadth, individual range was categorized into 1‰ bins (i.e.; 0<x≤1‰, 1<x≤2‰, etc.), and the proportion of individuals occupying each dietary type was calculated for each bin. To assess the influence of body size on individual breadth in δ13Cenamel, we tested for significant differences in the range of δ13Cenamel species of small (mass <100 kg), medium (100 kg ≤ mass <350 kg), and large (mass ≥350 kg) body size as well as the average range of individuals across these size categories. These categories are based on the commonly used and well-established body size categories of herbivorous mammals - based in part on dietary differences and also the prey sizes readily consumed by African predators (69-71). Body size estimates were made from the published literature, or new estimates were made based on allometries (Table S11). The potential influence of body size was assessed for the global dataset, the global dataset corrected for serial sampling bias, the dataset restricted to low latitudes (<37°), and the low latitude dataset corrected for serial sampling bias. Significant differences between average individual ranges according to dietary type was tested using Dunn’s test of non-parametric pairwise multiple comparisons.

Grazers tend to have higher-crowned teeth than browsers and mixed-feeders, and therefore tend to have more serial samples per tooth. To account for the possibility that more serial samples might produce a larger range of δ13Cenamel values, we performed a moving window analysis for each tooth, where we iteratively calculated the δ13Cenamel range for five consecutive samples, as denoted by each sample's distance from root along the tooth's growth axis. As an example, for a given tooth, we subset out samples 1-5, where one represents the sample closest to the root, and calculated the range of δ13Cenamel values. We then subset out samples 2-6, 3-7, and so on until the sample furthest from the root was included in a window. If multiple teeth were sampled from an individual, this procedure was applied separately to each tooth.

An Isotopic Individuality Index (III) was calculated for each taxon, as follows: Average individual range of δ13Cenamel (for a given taxon)/ Total δ13Cenamel range of the taxon. Average IIIs for dietary categories were calculated using only species-level data, unless it could be reasonably inferred that a genus was represented in the database by only one species (e.g., Camelops sp. in North America). Average IIIs were calculated at two scales: 1) at the global scale, and 2) restricted to individuals collected below 37° latitude (where C4 resources are primarily warm-season grasses and C3 resources are primarily trees and shrubs, in contrast to C3 ecosystems above 37° latitude were grass and browse cannot be discerned from isotopes alone (24, 25)). While we recognize that the latitudinal gradient in C3 and C4 grasses is likely a recent phenomenon, since ~5-7 Ma (23, 6572), there is no evidence from our analysis that any taxon is switching from C3 to C4 grass, seasonally or during the period of time during which their teeth mineralize (i.e., no teeth vary by ~14‰, the mean difference between C3 and C4 grasses; (23)). Thus, the analysis of δ13Cenamel values of individuals collected below 37° latitude is a reasonable proxy for inferring individual dietary variability.

We conducted variance partitioning analyses to quantify the proportion of δ13Cenamel variance that can be found between species, between individuals, and within individuals. We only analyzed those teeth with at least five serial samples. Individuals identified to the genus level were lumped with congeners identified to the species level only when it could be reasonably inferred based on location and geological time-period that they belonged to the same species (e.g. Mammutus sp. lumped with Mammutus columbi). Variance partitioning was done in two ways using R 4.0.2 (6673). (1) We fit via restricted maximum likelihood an intercept-only, nested ANOVA with δ13Cenamel as the dependent variable and individuals nested within species as random effects. This was done using the lme() function in the “nlme” R package (6674), and the varcomp() function in the “ape” package (6875) was used to extract the variance components. (2) We also partitioned variance (sum of squares) in δ13Cenamel using two-level, nested ANOVAs for unbalanced data following Ref. (37) (their Box 10.6, pp. 294-298).
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Figure 1. Stable carbon isotopic breadth of grazing, mixed-feeding, and browsing species. Hypothetical examples denote expected individual variability if individuals are specialists (left) or more generalized (middle). Empirical data (right, examples of serial samples from Supplementary Dataset) indicate that the average $\delta^{13}C_{\text{enamel}}$ range is 1.4‰ (1.1 SD, n=21; Supplementary Tables S1 and S2); grazing (green), mix-feeding (orange), browsing (blue).
Figure 2. Carbon stable isotope values from individual specimens of Cormohipparion emsliei from a 5 million-year-old fossil assemblage (Bone Valley, Florida, USA). Bulk and mean serial values (left) along with raw serial samples (right) exemplify broad dietary breadth as a species (range = 13.4‰), while individuals are highly specialized (all individuals sampled have ≤2‰ range of $\delta^{13}$C enamel, with an average $\delta^{13}$C enamel range of 1.1‰ Supplementary Tables S2 and S3). Obligate browsers (blue), obligate grazers (green), and all remaining mixed-feeders are indicated with other colors (orange-purple).
Figure 3. Proportion of individuals within serial-sample range bins per dietary group. Most serially sampled individuals (82.1% – 89%) regardless of dietary category, have δ¹³C enamel values that range ≤3‰ across when calculated using the full range of statistical methods. Only a small proportion of individuals (3.8% – 6%) range in δ¹³C enamel values by more than 5‰, all of which are grazers. The right skewed pattern is present whether we use A) the entire dataset, B) individuals with 5 or more serial-samples, or when we consider C) all samples below 37° latitude, and D) individuals that have at least 5 serial samples that are also restricted to below 37° latitude.
Figure 4. Isotopic Individuality Index (III) per dietary category. A) The overall species dietary range plotted against the average individual range for a species (one-to-one line given, species codes are defined in Table S7), and B) the distribution of III within dietary categories indicate a high degree of individual specialization (low index). Values closer to one are species in which the individuals are each more representative of the species as a whole, while smaller values indicate that individuals are specialized and less representative of their overall species dietary breadth. C) Below 37° latitude grazers plot near the one-to-one line more often than other groups; D) the III
for grazing species is higher than mixed-feeders below 37° latitude, and browsers at these lower latitudes are uncommon in this study.
Table 1. Summary statistics of dietary ranges for individuals, Isotopic Individuality Indices (III), and subsequent comparisons between groups using Kruskal–Wallis and Dunn’s tests.

| Dietary Category | Mean SD n | Comparison       | p-value |
|------------------|-----------|------------------|---------|
| Global Dataset   | Range     | Browser vs. Grazer | <0.001  |
| Browser          | 1.1 0.8  48 |                 |         |
| Mixed-Feeder     | 1.4 0.9  33 | Mixed-Feeder vs. Browser | 0.0629  |
| Grazer           | 1.8 1.5  231 | Grazer vs. Mixed-Feeder | 0.3785  |
| Below 37° Latitude | Range     | Browser vs. Grazer | <0.00001|
| Browser          | 1 0.7  19 |                 |         |
| Mixed-Feeder     | 1.5 1.0  32 | Mixed-Feeder vs. Browser | 0.0815  |
| Grazer           | 2.4 1.7  111 | Grazer vs. Mixed-Feeder | <0.01   |
| Global Dataset   | III       | Browser vs. Grazer | 0.5530  |
| Browser          | 0.35 0.17 7 |                 |         |
| Mixed-Feeder     | 0.18 0.11 4 | Mixed-Feeder vs. Browser | 0.1207  |
| Grazer           | 0.39 0.17 10 | Grazer vs. Mixed-Feeder | 0.0325  |
| Below 37° Latitude | III       | Browser vs. Grazer | 0.0475  |
| Browser          | 0.15 0.04 2 |                 |         |
| Mixed-Feeder     | 0.18 0.11 4 | Mixed-Feeder vs. Browser | 0.0164  |
| Grazer           | 0.44 0.11 6 | Grazer vs. Mixed-Feeder |         |

SD, standard deviation; n, number of individuals (in reference to range), number of species (in reference to III). Bold p-values are significant, <0.05.
Table 2. Variance partitioning analyses of individuals having at least five serial samples. Data are analyzed using both the entire dataset and samples from below 37° latitude. Treatment of individuals that were only identified to genus (published as "sp.") were "lumped" with congener individuals identified to the species level when it could be reasonably inferred that they belonged to the same species. The alternative was to treat "sp." "as is", or as their own taxon. The "REML" method uses restricted maximum likelihood fit a random effects nested ANOVA, while "SS" partitions sum of squares using nested ANOVAs for unbalanced data. The various levels at which variance is located are given, with the proportion of variance given for each dataset type, treatment, and method.

| Dataset | Treatment | Method | Between Species | Between Individuals | Within Individuals |
|---------|-----------|--------|-----------------|---------------------|--------------------|
| Global  | As Is     | REML   | 0.29            | 0.67                | 0.04               |
| Global  | As Is     | SS     | 0.31            | 0.64                | 0.04               |
| Global  | Lumped    | REML   | 0.34            | 0.61                | 0.05               |
| Global  | Lumped    | SS     | 0.57            | 0.38                | 0.05               |
| Below 37° | As Is   | REML   | 0.42            | 0.53                | 0.05               |
| Below 37° | As Is   | SS     | 0.38            | 0.57                | 0.05               |
| Below 37° | Lumped | REML   | 0.43            | 0.51                | 0.06               |
| Below 37° | Lumped | SS     | 0.63            | 0.32                | 0.06               |