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A community-informed list of key speciation concepts for undergraduate education

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Abstract

Background: Many topics in evolutionary biology have been the focus of little research about student thinking and learning. This lack of research limits the evidence base on which instructors can draw to inform their teaching. A key starting place for education research about evolutionary topics is determining what concepts are important for undergraduates to learn. This work develops a community-informed list of key concepts about speciation. Speciation is commonly taught in undergraduate biology education, yet has been the focus of almost no research on teaching and learning. We gathered input from over 110 evolution educators and speciation researchers to create a comprehensive list of speciation concepts for undergraduate education.

Results: The community-informed list includes 24 concept statements organized within 4 overarching concepts. At least 80% of experts rated these statements as scientifically accurate and clear. Over 90% of experts rated the statements as important or somewhat important for a graduating senior in biology to understand.

Conclusions: This list provides a foundation for both education researchers and evolution educators. Education researchers who investigate student thinking and who develop research-based measurement tools can use this list to determine key concepts on which to focus their future work. Educators can use this list to guide the development of learning objectives for speciation instruction. Future work should investigate what concepts are reasonable for an undergraduate to master in a 4-year degree.

Keywords: Speciation, Conceptual learning, College, Undergraduates, Evolution understanding, Standards, Key concepts

Background

Currently there is little research about teaching and learning many topics in evolution. A systematic analysis of peer-reviewed literature related to undergraduate evolution education revealed many gaps in our existing knowledge base (Ziadie and Andrews 2018). Specifically, there has been little (or no) research about student thinking and learning of numerous evolutionary topics, including macroevolution, speciation, population genetics, quantitative genetics, life history evolution, and more. In contrast, research on how students think about and learn natural selection and tree-thinking has been much more common (Ziadie and Andrews 2018). This trend has continued despite repeated calls for additional education research related to non-adaptive evolutionary processes and macroevolution (e.g., Padian 2010; Novick et al. 2014; Price and Perez 2016). The outcome of this under-emphasis is a limited evidence base on which instructors can draw to inform their teaching.

In addition to the underrepresentation of particular evolutionary topics in education research, few researchers have aimed to establish standards for what college students should learn about evolution (Ziadie and Andrews 2018). Standards, which could include key concepts for students to learn, are an important starting place for education research. Research that aims to investigate student thinking and learning, develop research-based measurement tools, or develop and evaluate specific instructional strategies must focus on

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particular concepts or skills related to an evolutionary topic. For example, researchers aiming to investigate how college students reason about population genetics must choose particular population genetics concepts to study. These decisions would be facilitated if important evolutionary topics were broken down into key concepts that were agreed to be important by the evolution education community.

Two efforts have made some progress in this direction. The team behind the "Understanding Evolution" website created a framework of age-appropriate evolution concepts across grades K-16 (Understanding Evolution Conceptual Framework). This framework is aligned with both the Framework for K-12 Science Education (NRC 2012) and Next Generation Science Standards (NGSS Lead States 2013). It includes concepts for undergraduates, but these concepts are much less extensive than the evolution topics commonly taught in upper-division evolution courses (Ziadie and Andrews 2018). Therefore, this framework is best aligned with introductory biology instruction. Another research team expanded on the five core concepts in Vision and Change (AAAS 2011) by generating a framework of specific conceptual statements. This framework, called the BioCore Guide, incorporated feedback from more than 240 biologists and educators (Brownell et al. 2014). It describes evolution concepts in more detail than the Understanding Evolution framework, but still excludes many of the evolution topics taught in upper-division courses (Ziadie and Andrews 2018). Thus, the existing frameworks are insufficient to guide researchers who want to investigate student thinking and learning about specific evolutionary topics.

Our work aimed to establish a list of key concepts related to an important and overlooked evolutionary topic: speciation. Speciation was taught in over 95% of surveyed upper-division college evolution courses, and yet has been the focus of only two papers about assessment (e.g., Nadelson and Southerland 2010; Romine and Walter 2014) and a handful of non-empirical papers presenting instructional strategies (Ziadie and Andrews 2018). Not a single paper has investigated how undergraduates think about and learn speciation, nor are there studies determining appropriate speciation concepts for undergraduates to learn.

Thus, we aimed to develop a community-informed and comprehensive list of key speciation concepts for graduating college students. We drew on the expertise of speciation researchers and college faculty who teach speciation to build and refine a list of concepts. We present this as an aspirational list of concepts to be taught in an undergraduate curriculum focused on evolution.

Methods

Generating initial statements

We generated a preliminary list of speciation concept statements by consulting various undergraduate evolution, biology, and genetics textbooks and relevant peer-reviewed literature. We used these resources to identify how educators and researchers defined and explained speciation concepts, which concepts they emphasized, and how they organized concepts. We iteratively refined this list as a research team to create succinct statements that could then be evaluated by the community. Our preliminary concept list consisted of five main statements that had two to eight sub-statements each, for a total of 24 concept statements. We presented these concepts to community members via a series of online surveys. We used an iterative series of three surveys to gather feedback and revise concept statements. We both added and removed concepts based on expert feedback. We returned to the literature as needed to gain further insight.

Participant identification and recruitment

We recruited speciation experts to provide feedback on the list of speciation concepts. We recruited participants in three rounds and each sample evaluated a slightly different list of key concepts. We recruited participants in the same way for each of the three surveys. We identified experts in two different ways. We recruited some experts who had taught speciation in an upper-division undergraduate course. We expected these individuals to have valuable insight about what concepts are important and reasonable for undergraduates to learn about speciation. These experts had to have taught in evolution in an upper-division course in the last 3 years. We identified these experts by searching for courses focused on evolution within institutions of higher education that grant 4-year degrees. We identified these institutions from the Carnegie website (Carnegie Classification of Institutions of Higher Education). We filtered the list of institutions to only include institutions that offered 4-year degrees. We randomized this list, started at the top, and proceeded down the list. For each included institution, we used the institution's website to identify relevant courses and the instructors who had taught that course in recent years. We then found those instructors' email addresses from their institution's website.

We also recruited experts who were active speciation researchers. We expected these individuals to have valuable input about what concepts are most important to the field. These experts had published peer-reviewed research related to speciation within the last 3 years. We identified these experts via peer-reviewed journals that publish research related to evolutionary biology including

The Journal of Evolutionary Biology, Evolution, Molecular Ecology, American Journal of Botany, New Phytologist, Systematic Entomology, Journal of Evolution, Ecology and Evolution, Molecular Biology and Evolution, Molecular phylogenetics and Evolution, and Current Zoology.

Though we recruited experts in two different ways, we expect many participants drew on expertise gained through both research and teaching. In total, we sent email recruitments to 706 potential expert participants in and outside of the United States. This included 211 faculty who had recently taught an upper-division course and 495 speciation researchers. Overall, 16% (n = 111) of those who received recruitment emails completed most or all of the survey about which they were contacted. Speciation researchers made up slightly more than half of the total expert participants (Table 1). Of 111 participants, many (70%) had taught speciation in an upper-division course in the last 3 years and 60% had recently published peer-reviewed articles related to speciation (Table 1). We conducted a total of three rounds of surveys and each expert participated in only one of these rounds. We opted for this approach to minimize the burden on any individual participant and to maximize the diversity of experts involved.

Data collection

We used three online surveys to gather expert feedback about the scientific accuracy, clarity, and importance of each statement of a speciation concept. The survey presented the concept list and asked experts to rate each concept as either "Accurate and clear" or "Inaccurate and/or Unclear." If a participant rated a concept as "Inaccurate and/or unclear," the survey prompted them to provide feedback about how to edit the statement to be scientifically accurate and clear. The survey also asked experts to rate each concept as "Important," "Somewhat important," or "Not Important" for a graduating senior in biology. Lastly, the survey presented the full list of concepts and asked experts if it was complete and, if not, what suggestions they had for additions. Each survey was identical except for the key concepts. See the full survey questions in the Additional file 1. We revised the list of key concepts and the articulation of each concept after Survey 1, and repeated the same process with a new and larger sample of experts in Survey 2. Experts responding to Survey 2 encountered only the revised key concepts, not the prior concepts. We made further revisions based on feedback collected in Survey 2 to create a list that a new sample of experts evaluated in Survey 3.

Table 1 Number of participants, recruitment approach, and teaching, by survey

	Number of participants	Recruited as researchers (%)	Recruited as instructors (%)	Taught evolution recently (%)[a]
Survey 1	12	0	100	100
Survey 2	50	88	12	52
Survey 3	49	47	53	82
Total	111	60	40	70

[a] All participants recruited as instructors and some participants recruited as researchers had taught evolution in an upper-division undergraduate course within the last 3 years

Data analysis

We calculated the percentage of experts from Survey 3 who rated each statement as "Accurate and clear," and the percentage who rated each statement as "Important" or "Somewhat important." Our cut-off for including a statement in our final community-informed key concept list was 80% of Survey 3 experts agreeing that the statement was "Accurate and clear." We chose 80% as our criterion for consensus, rather than something higher, for two reasons. First, species definitions and delimitations continue to be debated within the scientific community (e.g., Wheeler and Nixon 1990; Mayden 1997; de Queiroz 2007), so we expected some disagreement among the experts we surveyed. Second, we aimed to articulate fine-grained key concepts, potentially making consensus more difficult to achieve than for more general statements. In contrast, researchers creating the BioCore Guide and determining key concepts in evolutionary medicine aimed to craft more general statements. BioCore creators used a 90% cut-off for agreement of importance and scientific accuracy (Brownell et al. 2014), and the evolutionary medicine team accepted 80% of participants strongly agreeing or somewhat agreeing with the importance of a statement as a mark of consensus (Grunspan et al. 2017). In the end, we did not need to have a separate inclusion criterion based on importance ratings because experts reported that most statements were important for students to learn. The only statement about which there was substantial disagreement regarding importance also garnered disagreement about accuracy, and thus was excluded from the final list.

Results

The community-informed list of key speciation concepts produced by this work includes 24 statements organized within four overarching concepts (Table 2). Experts rated the full statements, and the research team generated the short codes for the sake of succinctly communicating data. More than 80% of experts responding to Survey 3 rated each of these statements as being "Accurate and clear," with two exceptions that

Table 2 Full key speciation concepts and short codes

Short code	Full key concept statements
SC1[a]	*A species is a population or group of populations that experiences evolutionary processes independently from other populations. Biologists use species concepts to draw boundaries between species, and develop tests of hypothesized species boundaries. No species concept is appropriate for all biological contexts and biologists often rely on more than one species concept to confidently determine species boundaries*
SC2	The criterion for determining species boundaries under the biological species concept is reproductive isolation. A species is composed of populations whose members are capable of mating and producing viable and fertile offspring, or would do so if they came into contact. Members from different species could not mate freely or could not produce viable and fertile offspring
SC3[b]	The criterion for determining species boundaries under the phylogenetic species concept is a unique combination of shared, derived character states. A species is composed of the smallest monophyletic group that shares a unique combination of derived characters that is different from all other populations
SC4	The criterion for determining species boundaries under the phenetic species concept is degree of phenotypic similarity, including morphological, physiological, or behavioral similarity. A species is composed of populations with shared phenotypes
SM1[a]	*Ultimately, speciation results from lack of gene flow between populations. When barriers to gene flow exist, populations will begin to diverge genetically because they independently experience mutation, selection, and genetic drift*
SM2	Lack of gene flow commonly occurs when populations are geographically isolated. This can happen when a large population is subdivided into two or more isolated populations because of the development of geographical barriers OR when one or more small populations are geographically separated from the main large population
SM3	Lack of gene flow can also result from chromosomal mutations. One example of this is mutations resulting in a change in number of chromosome sets. A daughter population that has four copies of chromosomes (tetraploid) generally cannot reproduce with a diploid parent population, creating an immediate barrier to gene flow. Another example is gene inversions, which are mutations that invert a section DNA within a chromosome. This change prevents recombination and thus acts as a barrier to gene flow
SM4	Genetic divergence can result from natural selection based on the environment, including differences in resources, habitat, and interactions with other species. This is called ecological speciation and it can occur when populations are geographically isolated and when they are not geographically isolated
SM5	Sexual selection can also contribute to genetic divergence. This can occur when changes in mate preference and secondary sexual traits within a population lead to assortative mating, such that individuals prefer to mate with other individuals of the same population
SM6	Genetic divergence between populations tends to increase as a result of genetic drift. The impact of drift on genetic divergence will be greater in smaller populations and populations that experience less gene flow
RB1	*Reproductive barriers are biological features of organisms that prevent species from interbreeding or from producing viable and fertile offspring*
RB2	Prezygotic reproductive barriers prevent gametes from meeting to form zygotes
RB2.1	Behavioral isolation is when differences in behavior prevent individuals of one species from mating with individuals of another species
RB2.2	Ecological isolation is when differences in habitat and resource use prevent individuals of one species from mating with individuals of another species. Examples of ecological isolation include differences in timing and location of breeding
RB2.3	Mechanical isolation is when differences in reproductive structures prevent the successful mating of different species
RB2.4	Gametic isolation is when transferred gametes of one species are unable to fertilize eggs of individuals of another species
RB3	Postzygotic reproductive barriers reduce the fitness of hybrids
RB3.1	Intrinsic postzygotic isolation is when hybrids exhibit biological problems that prevent them from producing offspring or reduce the viability or fertility of their offspring. These problems are independent of the environment. One example is incompatible interactions between genes inherited from parent populations
RB3.2	Extrinsic postzygotic isolation is when hybrids have lower fitness as a result of interactions between their biological features and the environment. One example is hybrids not surviving as well because they are not adapted to forage in the available habitats
OH1	*Secondary contact occurs when populations that have been geographically separated come back into contact with each other. Hybridization occurs when individuals from these formerly separated populations mate and produce offspring. Possible evolutionary outcomes of hybridization are hybrid zones and hybrid swarms, hybrid speciation, and reinforcement*
OH2	Hybrid zones are geographical areas in which individuals from distinct populations or species mate and produce hybrid offspring. Hybridization can lead to introgression, in which alleles from one population are incorporated into the gene pool of another population
OH3	If populations of hybrids survive beyond the first hybrid generation and continue to interbreed with parental populations, then these hybrid populations are called hybrid swarms. Hybrid swarms are often highly variable phenotypically and genetically due to gene flow between parental populations. A hybrid swarm can lead to the loss of distinguishable species, which is known as species collapse. This process can be exacerbated by human influences on habitats, including the introduction of invasive species and climate change
OH4	Hybrid speciation may occur if hybrid offspring have higher fitness in a habitat that is different from the habitat(s) of the two parent populations, and they are reproductively isolated from both parent populations
OH5	Reinforcement is natural selection that favors individuals who preferentially mate with individuals from the same population. This mating preference increases reproductive success when hybrid individuals have lower fitness than individuals from the parental populations. Reinforcement reduces the frequency of hybrids

Italics indicate overarching concepts

SC, speciation concept; SM, speciation mechanism; RB, reproductive barriers; OH, outcome of hybridization

[a] SC1 and SM1 are both versions of the statements from Survey 2. All other statements are from Survey 3

[b] SC3 was generated based on feedback from experts. The final version was not evaluated by experts

Table 3 Expert rating of key speciation concepts for accuracy and clarity, as well as importance

Short code	Accurate and clear (%)	Important (%)	Somewhat important (%)[a]
SC1	84[b]	88	12
SC2	92	86	14
SC3	NA	NA	NA
SC4	83	29	57
SM1	85	93	4
SM2	90	90	10
SM3	85	79	21
SM4	78	74	23
SM5	85	74	26
SM6	83	85	15
RB1	81	91	9
RB2	92	86	14
RB2.1	100	71	26
RB2.2	94	71	26
RB2.3	100	57	37
RB2.4	100	63	31
RB3	94	83	17
RB3.1	94	63	31
RB3.2	97	71	23
OH1	88	76	24
OH2	97	74	18
OH3	85	53	35
OH4	91	65	29
OH5	82	65	26

[a] Important and Somewhat important do not necessarily sum to 100% because experts could also rate a statement as "Not important"

[b] The number of experts evaluating each statement ranged from 33 to 50. The average number of experts evaluating each statement was 38

are described below. When asked to rate the importance of concepts for a graduating college senior to know about speciation, 91 to 100% of experts rated each statement as either "important" or "somewhat important" (Table 3). Most statements were rarely rated as "not important," including 10 statements that never received this evaluation from experts.

Two statements (SM4, SC3, Table 2) did not achieve the threshold of being considered accurate and clear by 80% of surveyed experts. One statement nearly reached this threshold (SM4, 78%, Table 3) and we opted to retain it in the final list so that researchers and educators could make their own judgement. Feedback from experts allowed us to propose a revision to the other statement, SC3, which is about the phylogenetic species concept. This statement required revision because only 63% of experts rated the version of the statement in Survey 3 as accurate and clear. Another version of this statement was rated as accurate and clear by 77% of experts in Survey 2. Expert feedback indicated the need to synthesize the statement versions from Surveys 2 and 3. Specifically, experts argued for the inclusion of diagnosability, which is the ability to recognize populations because they possess a unique combination of character states. They also valued the inclusion of monophyly and the existence of unique shared derived characters (apomorphies) in a statement of the phylogenetic species concept. Thus, as shown in Table 2, we propose a community-informed version of the phylogenetic species concept that includes both of these criteria. It is important to note that this version of the statement has not been evaluated by experts, but was created with expert feedback in mind.

Experts evaluated most of the final statements in Survey 3, but two were evaluated in Survey 2 (SC1, SM1, Table 2). Revisions to these statements between Survey 2 and Survey 3 decreased the proportion of experts who rated them as accurate and clear, so we retained the versions of the statements from Survey 2, in which 84% and 83% of experts rated as accurate and clear, respectively. Additionally, one statement about the ecological species concept was omitted from our final list entirely because repeated revisions based on feedback did not result in consensus among experts about the accuracy or the importance of the statement.

Discussion

This work lays a foundation on which evolution education researchers can build. We have identified a comprehensive list of speciation concepts that educators and researchers agree are important for biology graduates to understand. Researchers who study student cognition and learning can use this list to select specific speciation concepts to explore further. Research on student cognition and learning can then lay the groundwork for developing research-based measurements of undergraduates' thinking about speciation. Educators can use this list as they determine what concepts are key for their students to learn.

We offer one caution about the comprehensiveness of this list. This list represents the concepts that evolution experts see as important, but it does not consider what is feasible for undergraduates to master during a 4-year degree. It is possible that the level of the detail included in this list, if combined with this level of detail about other topics in biology, would be an unreasonable expectation for most undergraduates. It might be more reasonable to think that students develop this level of conceptual knowledge in the first years of graduate school. Thus, we present this list as tentative, and we encourage researchers to investigate how undergraduates learn these concepts, so that a final list of key speciation concepts is built not just from the expert perspective, but also from a student-centered perspective of learning.

A key concept list is only a starting place for speciation instruction. A critical next step will be aligning learning objectives with these key concepts. These concepts were not written nor evaluated to be statements presented to students. Furthermore, they do not illuminate what students should be able to do if they understand a key concept. For example, key concept SC2 describes the biological species concept. Most basically, instructors might aim for students to achieve this learning objective: "Define the biological species concept." We would advocate that upper-division courses aim for more advanced learning objectives, such as, "Use the biological species concept to evaluate data and determine if a population should be managed as one or more species." It will be important for the evolution education community to discuss and aim for consensus about how key concepts should be translated into concrete learning objectives.

We encourage researchers and educators to look closely at the data about importance (Table 3), which may suggest ways to limit this list to only the most critical concepts. If we used a cut-off of 80% of experts rating a statement as "Important," the key concept list would be reduced from 24 to 8 concepts. That said, experts were not asked to rank statements so these values do not represent relative importance. Rather, experts rated the importance of each statement independently, so statements with values greater than 80% were rated as important by more than 80% of experts. Some experts may have rated every key concept as important whereas others may have rated only some as important.

We anticipate that some readers will find fault with this list of speciation concepts. This potential for disagreement was reflected in our survey results. It was not uncommon for experts to provide feedback in direct contradiction to feedback from other experts. We offer this list of key speciation as a starting place that garnered approval from most, but not often all, surveyed experts. See Additional fiel 2 for the written feedback provided by surveyed experts and anonymous reviewers regarding each key concept in the final list.

We also discuss a few areas of disagreement among experts that influenced the final list of key speciation concepts. First, this list of speciation concepts does not explicitly name the various geographical contexts in which speciation may occur (i.e., allopatry, sympatry, parapatry). Early versions of concept statements emphasized how barriers to gene flow may arise within different geographical contexts and defined allopatric, sympatric, and parapatric modes of speciation. However, experts disagreed about the utility of discussing modes of speciation by focusing on geography, and instead advocated for greater focus on processes of speciation. Modern speciation research often focuses on different evolutionary processes that drive genetic divergence (e.g., Funk 1998; Mani and Clarke 1990; Ramsey and Schemske 1998; Schluter 2009; Maan and Seehausen 2010). This is partly because speciation research has progressed to the extent that the different evolutionary processes driving speciation can be tested directly (Butlin et al. 2008). SM2 (Table 2) recognizes that geographical isolation often contributes to speciation, and SM4 (Table 2) recognizes that natural selection can lead to speciation with or without geographical isolation. We do not dispute that geographic separation is important to speciation; nor did most of the surveyed experts. However, definitions of allopatric, sympatric, and parapatric speciation are not part of the key concept list.

We also want to highlight that though we have included species concepts in the community-informed list, this is an area of historical and ongoing debate. Different biologists have advocated the use of various species concepts, and the inconsistencies between these concepts can lead to differing conclusions concerning the number of species that exist. For example, Mayden (1997) identified 24 species concepts that he recognized as distinct, many of which are at least somewhat incompatible. Evolutionary geneticists and systematists both concern themselves with species and speciation, but focus primarily on understanding the processes of speciation and the taxonomy of diversity, respectively. These differing scholarly goals may lead them to advocate different concepts of a species. Thus, it is not surprising that this sample of experts—selected based on their expertise in speciation writ large—had diverse ideas about the utility of different species concepts and their relative importance.

Two experts in our study suggested the inclusion of the Unified Species Concept (de Queiroz 2007). De Queiroz (2007) argues that all species concepts include the common idea that species are a separately evolving metapopulation lineage, and that this should be the only necessary property of species. Other properties, such as reproductive isolation and monophyly, would then be considered different lines of evidence for assessing lineage separation that can be acquired by lineages as they diverge (de Queiroz 2007). Ultimately, we did not include a key concept statement explicitly about the Unified Species Concept. Instead, statement SC1 describes species as "a population or group of populations that experiences evolutionary processes independently from other populations" (Table 2). We recommend that upper-division speciation instructors consider how the ideas of de Queiroz (2007) fit into their courses and consider the 2007 paper as a possible introduction for students to the diversity of and disagreement regarding species concepts.

De Querioz is not alone in suggesting that different species concepts address fundamentally different entities (e.g., Ereshefsky 1992, Baum and Shaw 1995). For example, Harrison (1998) proposes that the phylogenetic species concept and biological species concept can be viewed as different stages in the speciation process and that the order of these stages may vary based on the geography of speciation. These discussions may have a place in upper-division courses.

There are other resources specifically written for educators and students that may usefully supplement traditional textbook readings in introducing students to key speciation concepts. *Understanding Evolution* is an education website that provides both readings and lesson materials related to evolutionary biology (https://evolution.berkeley.edu/evolibrary/home.php). The resources therein are particularly useful for lower-division undergraduate courses. Other resources target more advanced students. *Scitable by Nature Education* (https://www.nature.com/scitable) includes articles written for students on topics in evolutionary genetics. For example, Johnson (2008) addresses hybrid incompatibility and speciation, Stevison (2008) discusses hybridization and gene flow, and Hey (2009) discusses species concepts. Similarly, *eLS Citable reviews in the life sciences* (http://www.els.net/WileyCDA/) includes overviews of topics in evolution written at appropriate levels for college instructors and students. These vary in specificity from an overview of species concepts by Ghiselin et al. (2010) to an evolutionary history of polar and brown bears by Hailer and Welch (2016). eTS resources require access to Wiley Library Online.

Conclusions

This paper presents a community-informed list of key speciation concepts. We hope it will prompt additional research and discussion about the understandings we aim to cultivate in students earning a degree in biology. We also hope it offers a jumping off point for research about how undergraduates think about these important speciation concepts. Researchers would benefit from a research-based assessment of student thinking about speciation that is grounded in the concepts valued by the community. Educators can use this list, or parts of it, as a conceptual framework for planning learning objectives for students.

Additional files

Additional file 1. Survey used to gather expert feedback on speciation concepts.

Additional file 2. Written comments provided by surveyed experts and anonymous reviewers regarding each key concept in final list.

Abbreviations

SM2: speciation mechanism 2; SM4: speciation mechanism 4; SC3: speciation concept 3; SC1: speciation concept 1; SM1: speciation mechanism 1.

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Authors' contributions

DD helped conceptualize the study, collected and interpreted data, and drafted the manuscript. NE helped conceptualize the study, collected and interpreted data, and drafted the manuscript. TCA conceptualized the study, interpreted the data, and drafted the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data analyzed in this manuscript is available upon request from Tessa Andrews (tandrews@uga.edu)

Ethics approval and consent to participate

The Institutional Review Board of the University of Georgia determined this work (#00003496) was exempt.

Competing interests

The authors declare that they have no competing interests.

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