Ecological Genetics of Speciation and Adaptation—Spring 2013

PLB/Zool 849. Doug Schemske. schem@msu.edu

Tuesday, March 12

Class objectives, introduction to speciation.

Thursday, March 14

Introduction to speciation continued.

Reading:

Schluter, D. 2001. Ecology and the origin of species. Trends Ecol. Evol. 16:372-380.

Sobel, J M., G. F. Chen, L. R. Watt and D. W. Schemske. 2010. The biology of speciation. Evolution 64: 295-315.

Tuesday, March 19

Introduction to speciation continued, discussion of readings.

Reading:

Noor, M. A. 1995. Speciation driven by natural selection in *Drosophila*. Nature 375:674-675.

Rundle, H. D., L. Nagel, J. W. Boughman and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. Science 287:306-308.

1. Are mating discrimination and hybrid inferiority the principal reproductive isolating factors in Noor's *Drosophila* system? If not, what other factors should be considered? Why?
2. What is the mechanism of reproductive isolation investigated by Rundle et al.?
3. Are the sticklebacks studied by Rundle et al. different species?

Thursday, March 21.

Discussion of reading. **Read both of the papers below**.

***** Write a review of ONE paper, due in class** (**2-3 pages, Times New Roman, 11 font, double spaced**). See attached guidelines and sample review.

Savolainen, V., M. Anstett, C. Lexer, I. Hutton, J. J. Clarkson, M. V. Norup, M. P. Powell, D. Springate, N. Salamin and W. J. Baker. 2006. Sympatric speciation in palms on an oceanic island. Nature 441: 210-213.

Schliewen, U. K., D. Tautz and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368: 629-632.

General questions to consider:

1) Are the ecological differences between the palms studied by Savolainen et al. and the cichlids studied by Schliewen et al. a signature of sympatric speciation?
2) Could the extinction of ancestral populations alter the conclusions presented in these papers?
3) What do you think were the first characters to evolve in cichlids and palms, and were these sufficient to begin the process of sympatric speciation?
4) Are there alternative explanations for the data presented in these papers?

Schliewen et al.

1) Do Schliewen et al. provide a good case for sympatric speciation?
2) What are the limitations of the phylogeny presented by Schliewen et al.?

Savolainen et al.

1) How accurate is the molecular dating? How might past hybridization affect the estimate of time since divergence?
2) How many fixed genetic differences do we expect between biological species? Are 4 of 274 enough?
3) Are the ecological differences they observe any different in kind or magnitude from what might be expected for allopatric speciation?
4) Can we really exclude the role of previous volcanic islands?

Tuesday, March 26

Introduction to adaptation.

Reading:

Barton, N. H. and P. D. Keightley. 2002. Understanding quantitative genetic variation. Nat. Rev. Genet. 3:11-21.

Thursday, March 28

Introduction to adaptation continued.

Reading:

Stinchcombe, J. R. and H. E. Hoekstra. 2008. Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. Heredity 100: 158-170.

Tuesday, April 2

Discussion of reading. **Read all of the papers below**.

Barrett, R. D. H., S. M. Rogers and D. Schluter. 2008. Natural selection on a major armor gene in threespine stickleback. Science 322:255-257

Bradshaw, H. D., Jr. and D. W. Schemske. 2003. Allele substitution at a flower color locus produces a pollinator shift in two monkeyflower species (*Mimulus*). Nature 426:176-178.

Hoekstra, H. E., R. J. Hirschmann, R. A. Bundey, P. A. Insel and J. P. Crossland. 2006. A single amino acid mutation contributes to adaptive beach mouse color pattern 313: 101-104.

Thursday, April 4

***** Research proposal due in class (4 pages text, 1 page literature cited, double spaced).**

Lecture and discussion: Speciation and diversification in the tropics.

Readings below provide background (all optional):

Mittelbach, G. G., D. W. Schemske, H. V. Cornell et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecology Letters 10:315-331.

Schemske, D. W. 2009. Biotic interactions and speciation in the tropics. pp. 219-239, *In* Speciation and patterns of diversity, R. K. Butlin, J. R. Bridle and D. Schluter (eds.). Cambridge University Press, Cambridge.

Schemske, D. W., H. V. Cornell, G. G. Mittelbach, K. Roy and J. M. Sobel. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution and Systematics 40: 245-269.

Questions to consider:

1. Is speciation faster in the tropics? If so, why?
2. Is ecological isolation more important in the tropics?
3. Does diversity beget further diversity? If so, how?
4. How might we determine the role of history in explaining the latitudinal gradient?
5. Are biotic interactions stronger in the tropics?
6. How might biotic interactions contribute to speciation? To diversity?

Tuesday, April 9

***** Review of research proposal due in class** (**1 page, single-spaced**).

Panel discussion of proposals, decisions on funding.

[*** indicates assignment due in class]

Grading—Schemske's part:

1. review of paper	**5 points**
2. research proposal	**15 points**
3. review of research proposal	**5 points**

Some Guidelines for Writing Your Review
Due in class --March 21

Peer review is an essential part of the scientific process because it provides a mechanism for the findings of research projects to be evaluated as they are submitted for publication. Reviewers provide journal editors with written comments about the papers they review, and make recommendations about the acceptability of the papers. The authors typically receive a copy of the reviewers' comments, and these can help the authors improve their paper and develop their subsequent research. Although the paper you will review has already been published, you should act as if you are reading a draft version of the paper prior to its publication.

Your job is to provide constructive criticism/praise that can be used by the editor in making a decision on whether to accept the paper for publication, and by the authors in revising their paper. This requires highlighting both the strengths and weaknesses of the paper. Your **2-page review** (**double spaced, Times New Roman, 11 font**) should focus primarily on the broad, conceptual issues presented in the papers (not the minor details), and should address the following questions:

1) Are the questions posed in the paper clearly stated, and do these questions have broad significance for our understanding of evolution? If so, why? If not, why not? Spell out the significance of the paper to the field of evolutionary biology.

2) Are the methods used to investigate these questions adequate? If not, what kinds of observations and/or experiments would be useful? If you suggest specific sampling or experimental methods, try to indicate how these would contribute to the study.

3) Are the conclusions supported by the data? If not, what further research might be needed to provide additional data?

4) Are there other explanations of the results that the authors did not consider? If so, what are they, and do they invalidate the authors' conclusions? When identifying potential difficulties with the author's reasoning or conclusions, identify the exact problems and provide alternate interpretations.

5) Do the findings presented in the paper improve our understanding of the evolutionary process? Why?

Sample Review

The subject of this paper is the role of local adaptation in the evolution of reproductive isolation among populations. This is an important and interesting topic, given the increasing awareness that ecological factors may play an important role in speciation—a view first proposed in detail by Mayr (1947). As the author correctly notes, most studies of speciation have focused on comparisons of current species, and this is fraught with difficulties, as reproductive isolating factors that had nothing to do with the original speciation event will continue to accumulate. This, it is nearly impossible to determine what role current barriers may have played during divergence. Hence, the focus of the manuscript on divergence among populations within a species is a good first step towards identifying the factors that might contribute to the earliest stages of divergence.

While the data set presented in the present paper is important and should be published, the paper in its current form is not acceptable. There are a number of problems in methodology, analysis and interpretation that need to be addressed.

1) Six populations are investigated, two from each of three habitat types. The paper examines the hypothesis that populations from the same habitat type will display less reproductive isolation (post mating, postzygotic) than will populations from different habitat types. The justification for this view is that reproductive isolation (RI) will evolve as a byproduct of local adaptation. However, this assumes that populations of the same habitat type possess the same ancestry, and therefore have the same genetic basis for adaptation. This need not be the case, and is particularly so for a highly selfing species like the subject of the study. Therefore, what is really needed is information on the genetic relationships among populations-- then genetic distance can be used as a covariate.

Related to this, one can also imagine that spatial distance between populations might correlate with genetic distance, so this too should be considered in the analyses and interpretations, yet I could not find any discussion of this point.

2) More justification is needed to support the hypothesis that local adaptation to edaphic factors will result in RI for premating isolation.

3) The main argument is that local adaptation drives the evolution of RI, and if so, then why not simply examine the relationship between RI and the degree of local adaptation for pair wise combinations. It sounds like the author has these data in his dissertation. Instead, the present paper seems to rely on the assumption that populations occupying similar habitats will also display less local adaptation than those occupying different habitats. That might be true, but if the adaptive traits evolved multiple times, then there is no reason to assume the relationship proposed by the author. In any event, aren't the data available to test this?

4) It seems a bit odd that the paper focuses on the consequences of local adaptation for the evolution of RI, without recognizing that local adaptation in itself represents a form of RI. If populations are locally adapted, then adaptive genes that might move between populations are weeded out by selection. Here again, it would be interesting to know the degree of local adaptation.

5) Several papers in the past few years have estimated several components of RI, and have attempted to estimate the total RI between species and populations. This is complicated, since once can never measure all components. Nevertheless, it would be interesting to provide a measure for the two components presented in the study, and for that due to local adaptation. Obviously, the expectation is that total RI is less than one. Here again, one really wants to know the relationship between total RI and genetic distance. Biological species have total RI>1.

6) More discussion is needed of the role that mating system might play in the evolution of RI in the system. The study species appears to be highly selfing (it would be very useful to now just how much selfing it does), so I'm not sure that postmating or even post zygotic measures of RI are meaningful. Imagine a completely selfing "species": (admittedly, there is no such thing). In any event, why would we use the potential for gene flow between populations as an indicator of RI between two lineages that never exchange genes? Coyne and Orr suggested that mating system should not be treated as an isolating mechanism, since the degree of isolation between populations that is caused by selfing is the same as that between individuals of the same population. They have received some opposition for this, but I think they are right. In any event, the author needs to give this issue some serious thought. I would argue that the degree of local adaptation between populations is perhaps a better indicator of "ecological" species in a selfer than is the degree of post mating or postzygotic isolation, though I recognize many would disagree. Critical questions: What is a biological species in selfing lineages? For selfers, what are the most important criteria for "isolation"?

Other points indicated by page/row number:

p 9—"The pollen recipient was pollinated by an individual from the same population, a plant from a different population but the same habitat type, and by two plants from populations of a different habitat type." Not sure what the latter section means—one habitat type? Why two plants?

p 10-11. "I also tested the hypotheses that individual populations differed in their ability to successfully pollinate plants from other populations and that specific pairs of populations showed evidence of postmating isolation." this will almost certainly be true, but I do not see what the conceptual motivation for this is, or what it tells us about the relationship between speciation and adaptation.

p. 14, 15—"If postzygotic barriers are associated with habitat differences, purebred and intra habitat hybrids will have similar fitness, and both will have significantly greater fitness than inter-habitat hybrids." as I suggested above, one would expect that individuals from the same population are more closely adapted to their habitat than are individuals from different populations, even though they may seem to occupy similar habitats. Thus, why not expect less RI in purebred crosses?

Research proposal for the study of speciation or adaptation

Due date--April 4 (in class)

Prepare a short research proposal in which you describe a project to investigate the mechanisms of speciation or adaptation in any group of organisms.

Your proposal should include **4 pages of text and one page of literature cited, all double-spaced and in Times New Roman, 11 font**. Your proposal must include the following sections:

I. Conceptual overview
II. Background to the study system
III. Hypotheses and rationale
IV. Experiments and observations
V. Intellectual merit (= significance of the proposed research)
VI. Literature Cited

DO NOT PUT YOUR NAME ON THE PROPOSAL—USE A CODE WORD!!!

I will circulate the proposals for review in class on the due date. Each student is responsible for reading and reviewing one proposal. Your review should first address the question: **What is the intellectual merit of the proposed research?** Then provide a brief summary statement that gives a description of the research, its major positive and negative aspects, and your final recommendation. Bring the review (**1 page, single-spaced**) to the class meeting on **April 9.** At this time, we will establish several review panels, and the members of each group will discuss the merits of the proposals they have reviewed. The goal is to select one proposal from each group to receive funding from *The Schemske Endowment for Evolutionary Studies*. Each group will then present a brief summary of the winning proposal. All proposals will then be returned to Schemske by the end of the period and he will conduct his own evaluation. He regrets that due to budget deficits and his huge boat payments, he will be unable to fund any of the meritorious proposals in this round of competition. **Attach the Proposal Review Form** (see last page) to your review.

Proposal Review Form: ***The Schemske Endowment for Evolutionary Studies***

Attach this rating form to your review of the proposal (1 page, single-spaced, Times New Roman, 11 font).

Reviewer's name _____

Proposal code name _____

National Science Foundation (NSF) seeks to support the most meritorious research whether basic or applied, to meet its statutory responsibilities. Reviews play a key role in the NSF's evaluation of research proposals.

Institution: Michigan State University

Overall Rating

- ☐ **Excellent** Outstanding proposal in all respects; deserves highest priority for support.
- ☐ **Very Good** High quality proposal in nearly all respects; should be supported if at all possible.
- ☐ **Good** A quality proposal, worthy of support.
- ☐ **Fair** Proposal lacking in one or more critical aspects; key issues need to be addressed.

- ☐ **Poor** Proposal has serious deficiencies.