Species and Speciation

BIOD62

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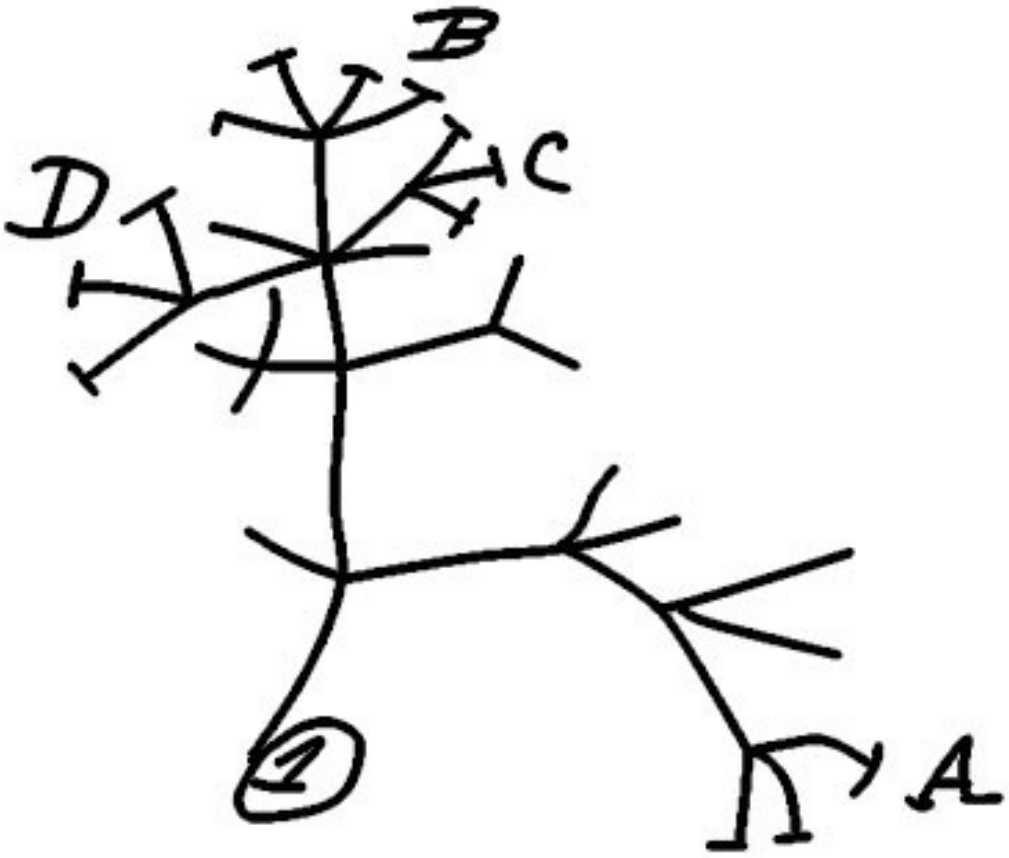

Course Manual, 2014

Course description

Speciation is one of the most basic and important processes in evolutionary biology by which new species arise. The purpose of this course is to learn about the main mechanisms behind speciation and their causes. We will first discuss the life and teachings of Charles Darwin, the father of modern evolutionary biology, and how his ideas about natural selection and the origin of species were validated in the 20th century (Modern Synthesis). As a basis for all following chapters, the course will then discuss genetic variation and different species concepts. We will then dissect different geographic speciation models, i.e. allopatric, peripatric, parapatric and sympatric speciation. Then time will be dedicated to the different mechanisms of prezygotic reproductive isolation. For example, species which are ecologically isolated typically only occur and mate in their preferred habitat, minimizing gene flow between incipient species. Temporally isolated species have different temporal mating windows, while behaviorally isolated species may meet, but one species does not recognize the sexual cues of the other species and hence the two species do not mate. The course will then discuss the range of postzygotic isolating mechanisms, such as extrinsic and intrinsic postzygotic isolation. We will learn about reinforcement, a process by which natural selection increases reproductive isolation of incipient species, typically when two populations have been separated for a long time and then come back into contact. Upon such secondary contact and with incomplete reproductive isolation, mating between such taxa might produce unfit hybrids, which drives natural selection to enhance prezygotic reproductive isolation between these incipient species. The course will then discuss the importance of drift and natural selection as the main driving forces of speciation. Speciation sometimes occurs in a 'sudden burst' and into different ecological niches. This process is referred to as adaptive radiation, the penultimate topic of the course. The last topic will cover diversity through time and also discuss the flipside of speciation, ie extinction.

Course objectives

This course aims at communicating the science behind 'species and speciation' through both lecture and tutorial time, with the latter tightly paralleling the former. In both lecture time and tutorials, there will be a strong emphasis on active and deep learning, thus you are expected to come prepared to tutorials, and to actively participate in group learning activities. This dual approach of the course aims at teaching '*science literacy*' and '*science communication*.' Assignments associated with these goals are: **a written paper** (scientific data interpretation and writing skills), and **a PPT presentation** on a published paper (oral skills). Another important skill this course aims at is how to give and receive peer feedback (for the paper and presentations; in tutorials).

(1) Paper. In a tutorial, Ivana Stehlik will provide in-depth information on how to write a good science paper. Building on this information, you will write a paper based on a published, but stripped-down data set on biogeographic speciation models. You will thus be provided with original data tables and/or figures from a published paper, while the paper source (authorship and text) will remain undisclosed. Each student will write a draft of the paper along with providing six key references. During a next tutorial and in a group-based, active-learning process, each student will provide and receive fellow student feedback on his/her paper draft with enough time to implement these suggestions before the deadline of the final paper submission. Similarly as for the in-class presentation, I encourage the group members to enter a contract ensuring a thorough peer review and time compliance.

(2) PPT presentation (during tutorials). In a first tutorial, Ivana Stehlik will provide in-depth information on how to prepare and present a good scientific PPT presentation. Together with a student

of your choice, you will then prepare a draft version of the PPT presentation and present it in a next tutorial to two peer reviewers, while also acting as a peer reviewer in return. You will then have enough time to implement the suggestions provided by the peers. In a next tutorial you will present the final version of the PPT to the whole class.

Course details

Instructor: Ivana Stehlik
Phone: 416-287-7422
Email: ivana.stehlik@utoronto.ca
Office hours: SW563C, TBA
Course lecture time and place: Mon, 2 - 4 PM
Tutorial time and place: Wed, 1-3 PM
Prerequisites: BIOC50. This is non-negotiable

Marks breakdown

Midterm exam (open book)	20%
Final exam (cumulative; open book)	33%
Data paper	18%
Feedback on draft of peer	6%
PPT presentation	18%
Tutorial attendance*	3%
Quiz on meiosis	2%
Total	**100%**
Optional brush-up Blackboard quiz on genetic drift, bottleneck and founder effect	2%

*Automatic full mark allocation for full tutorial attendance

Website

Class information will be provided on the course website on the U of T Portal: portal.utoronto.ca. You will need your UTORid and your password to access the site. Please refer to instructions on how to access the course website on blackboard using the information in http://www.portalinfo.utoronto.ca.

Lectures and other course material

Lectures and other course material (e.g. material to prep in-class presentations or the data set forming the basis of the paper) will be posted in a dedicated BIOD62H class folder on dropbox, so you will either need to create a new (and free) dropbox account or you can use your pre-existing dropbox. In order to create your personal 2 GB dropbox account, please follow instructions on the provided website by choosing the FREE option:

https://www.dropbox.com/pricing

Once you own a dropbox account, you will be able to follow the invitation sent to you by the instructor through email to join the dropbox class folder in the first week of classes. This invitation will be sent to your official university email account, so it is vital that you check your email inbox as soon as the course starts (no lecture material will be posted on Blackboard or intranet, so it is in your own interest to get access to all course materials through dropbox ASAP). Lectures will be posted typically the evening before class.

Course schedule/Important dates

Week, day, date	Lectures	Activity
1, Mon, 1/6	1/2	Darwin and the Modern Synthesis
1, Wed, 1/8	Tutorial	"How to write a good paper"
2, Mon 1/13	3/4	Genetic variation and mutation; Species concepts
2, Wed, 1/15	*No tutorial*	
3, Mon, 1/20	5/6	Allopatric and peripatric speciation
3, 1/20, 11:59 PM	**Choose your paper topic and email your 1st, and 2nd choice to Ivana Stehlik**	
3, Wed, 1/22	*No tutorial*	
4, Mon, 1/27	7/8	Parapatric and sympatric speciation
4, Wed, 1/29	*No tutorial*	
4, 1/31, 11:59 PM	**Send your paper draft as an email attachment to your two student peers for peer review**	
5, Mon, 2/3	9/10	Ecological isolation
5, Wed, 2/5	*No tutorial*	
6, Mon, 2/10	11/12	Behavioral and non-ecological isolation
6, Tue, 2/11	**Finish review of the two paper drafts of your two allocated peers**	
6, Wed, 2/12	Tutorial	Student-group based paper-feedback session
7	**Reading week**	
7, 2/23, 11:59 PM	**Submit your paper to turnitin**	
8, Mon, 2/24	Hand in meiosis quiz to Ivana Stehlik during class	
8, Mon, 2/24	13/14	Postzygotic isolation
8, Wed, 2/26	Tutorial	"How to make and give a good PPT presentation"
9, Mon, 3/3	Q/A	Lectures 1-12
9, Wed, 3/5	**During tutorial time: Midterm exam (lectures 1-12)**	
10, Mon, 3/10	15/16	Polyploidy and hybrid speciation
10, Wed, 3/12	Tutorial	Student-group based PPT-feedback session
11, Mon, 3/17	17/18	Reinforcement
11, Wed, 3/19	Tutorial	PPT presentations I
12, Mon, 3/24	19/20	Evolution of postzygotic isolation; Importance of selection vs drift
12, Wed, 3/26	Tutorial	PPT presentations II
13, Mon, 3/31	21/22	Adaptive radiation; Diversity through time – extinction
13, Wed, 4/2	Tutorial	PPT presentations III
Apr TBA (exam period)		**Final exam (lectures 1-22)**

Attendance policy in tutorials

In contrast to lectures, attendance will be taken in all tutorials. If you miss tutorials due to illness or other causes beyond your control, submit, within one week of the missed lab, a written request for special consideration to the instructor explaining the reason for missing the event, and attaching appropriate documentation, such as the official University of Toronto medical certificate (www.utoronto.ca/health/form/medcert.pdf).

If you attend all tutorials, you will be granted an automatic 5% towards your final grade. There will be no partial grade for partial attendance, as this part of the final grade aims at optimizing the learning outcome in group-based activities, which rely on predictable student attendance and participation.

Penalty for late submission

There will be a penalty of 10% per day for assignments received late. Weekend days count as individual days. Unless there are extenuating circumstances (e.g. medical reasons with a medical certificate), a mark of zero will be applied to assignments submitted one week late or more. Heavy workloads or malfunctioning computer equipment are not legitimate reasons for late submission. If you know ahead of time that you have a legitimate reason why you cannot hand in the assignment, let the course instructor know before the due date.

Missed exams

Students who miss an exam for reasons entirely beyond their control may, within one week of the missed test, submit a written request for special consideration to the instructor explaining the reason for missing the test, and attaching appropriate documentation, such as the official University of Toronto medical certificate (www.utoronto.ca/health/form/medcert.pdf).

Academic integrity policy

According to Section B of the University of Toronto's *Code of Behaviour on Academic Matters*, it is an offence for students to:

• use someone else's ideas or words in their own work without acknowledging that those ideas/words are not their own with a citation and quotation marks, i.e. to commit plagiarism.

• include false, misleading or concocted citations in their work.

• obtain unauthorized assistance on any assignment.

• provide unauthorized assistance to another student. This includes showing another student completed work.

• submit their own work for credit in more than one course without the permission of the instructor

• falsify or alter any documents required by U of T. This includes, but is not limited to, doctor's notes.

• use or possess an unauthorized aid in any test or exam.

Violation of the Code of Behaviour on Academic Matters will force the instructor to provide a written report of the matter to the Chair/DeanProvost's and a penalty according to the U of T's guidelines on sanctions will be put into place.

Submission of paper to Turnitin

Students will be asked to submit their paper to **Turnitin.com** for a review of textual similarity and detection of possible plagiarism. In doing so, students will allow their essays to be included as source documents in the Turitin.com reference database, where they will be used solely for the purpose of detecting plagiarism. The terms that apply to the University's use of the Turnitin.com service are described on the Turnitin.com web site:

(http://www.utoronto.ca/ota/turnitin/ConditionsofUse.html)

Turnitin.com is most effective when it is used by all students; however, if and when students object to its use on principle, the course offers a reasonable offline alternative. You will then be asked to meet with the course instructor to outline and discuss the report before its final submission to demonstrate the process of creating the report according to the academic integrity policy.

Communication policy

Students are required to regularly and often check their UTOR email to receive announcements or updates relating to the course. To inquire about course-related issues, students are strongly encouraged to solely use their UTOR email, as hotmail or other email providers are spam-filtered on a regular basis. It is the responsibility of you as the student to make sure your email reaches the instructor.

The instructor will not answer any questions related to material discussed in class or during the tutorials by email (unless it is a clear yes-no answer), but you are encouraged to ask these questions before or after class or the tutorial, during official office hours or to schedule a meeting outside office hours by email.

Accessibility

Students with diverse learning styles and needs are welcome in this course. In particular, if you have a disability/health consideration that may require accommodations, please feel free to approach the course instructor and/or the AccessAbility Services Office as soon as possible. Enquiries are confidential. The UTSC AccessAbility Services staff (located in SW302) are available by appointment to assess specific needs, provide referrals and arrange appropriate accommodations (416) 287-7560 or ability@utsc.utoronto.ca.

Readings

There is no required reading, but most topics introduced in the lectures are covered in the book [Coyne and Orr. 2004. Speciation. Sinauer], which is the recommended course book. The book is available at UTSC's book store (hopefully both new and used books). The course's approach in regard to exam questions is as follows: questions will only cover material introduced in class or labs. If you do not understand certain concepts, the recommended sections of Coyne and Orr's book should be consulted, but anything present in the book yet not covered in the lectures will not be on the exam.

In case a certain topic is not covered in Coyne and Orr's book, the lecture material originated most probably from primary scientific literature. In each such case, there is a reference provided on the slide along with e.g. a table or figure. This reference will help you to find the article using either ISI web of science (with your UTOR ID and password, on the website of the Gerstein library; http://www.library.utoronto.ca/gerstein/) or through Google scholar (does not work in all cases).

Assignments

1. Data paper

Potential topics for papers

The data paper will be on the topic of biogeographical speciation models (allopatric, peripatric, parapatric and sympatric speciation). There are three paper topics to choose from (data paper I, data paper II and data paper III). Please check out the material associated with the three choices on the course Blackboard website under 'Contents → 'Data papers') and email your first choice to ivana.stehlik@utoronto.ca by TBA (see timing in table on page 4 of syllabus). On a first-come-first-serve basis, each topic will be allocated to a third of the class.

Steps in the paper-writing process

In-course. In a tutorial, you will be provided in-depth information on how to write a good science paper. Building on this information, you will have to write a paper based on a published, but stripped-down data set on biogeographic speciation models, i.e. you will be provided with original data tables and/or figures from a published paper, while the source (authorship and text) of the paper will remain undisclosed. Before coming to the next tutorial, you will have to write a draft of the paper along with providing six key references. During this next tutorial and in the group-based, active-learning process, you will provide and receive feedback by two fellow students with enough time to implement these suggestions before the deadline of the paper submission.

On your own; work on your own data paper. You will get access to a ppt file (in dropbox) containing a brief outline of the speciation scenario, the questions involved and the data (figures and tables) needed to answer the outlined questions. The main question is the same for all three data options, i.e. you will need to figure out what biogeographical speciation model applies to a given scenario.

Here are some suggested steps on how to go about writing this paper. First, you will need to consult your lecture notes and read up on the four basic biogeographical speciation models (allopatric, peripatric, parapatric and sympatric speciation) in order to be familiar with what they are and on what means to distinguish between them. Then decide what model applies best to your chosen data scenario. Then start thinking what comparing evidence you will need to write an effective introduction and make your case for your chosen model in the discussion. Before you start writing your draft, please carefully read through the hand-out and ppt provided during the first tutorial on how to write a good paper, as these will help you in the writing process!

On your own; work on the data papers by your two allocated fellow students. Using the instructions on how to write the data paper provided in the first tutorial, carefully read through the two data papers and check whether and how well your fellow students have implemented the instructions.

In particular and beyond formatting and writing style, ask yourself whether you understand the argumentation in the papers and whether the argumentation is well enough supported by published literature. Focus on the abstract, introduction and discussion. Make notes/comments as you read along. It will probably work best if you insert your comments in the electronic word file using the function 'New comment' under the header 'Review' and then print off the file as a hard copy to bring to class and to give to the author of the paper. Limit your review process per paper to a max of 1h per paper.

Please refer to the table on page 4 in the syllabus for important deadlines in the process of the data paper writing!

Penalties for non-compliance in the paper-writing process

Because this whole peer review process only works if everybody does all steps involved on time, there will be a cumulative 10% penalty per day late for the deadlines of Jan 20, Jan 24 and Feb 3 (unless you bring a valid doctor's note).

This means specifically that if you send in your paper late to your fellow students for peer review, you will get 10% off your final paper mark for each day late. Also, if you fail to bring feedback comments to the tutorial dedicated to the peer review discussion, you will be penalized by ___ % (you decide as a group) off your final paper mark. And if you fail to send in your final paper to turnitin, you will be

penalized 10% per day late. In order to implement the deadline where I as the instructor am not involved (receiving the two papers in time the for peer review), please notify Ivana Stehlik by email.

Example of contract between group members to diminish likelihood of free-loading
A contract might not be necessary if you work with your best friend in a group of two, but is probably a good idea when working in a group with more than two members. The wording below is just a suggestion, so feel free to modify and complete it as a group. This contract can also be found in our course dropbox → modify if needed, print off and sign.

Rules for the data paper assignment
I hereby agree that I will do all that is needed to participate fully as a group member to give and receive feedback on the data paper.

In particular, I will…

☐ send the draft of my paper to my peer reviewers on time (timing see table on page 4 in the syllabus); deduction for non-compliance: 10% on the final mark for this assignment

☐ provide critical feedback to my reviewees to the best of my abilities, taking into account the rules and suggestions as provided by Ivana Stehlik in the 'how to write a good scientific paper' tutorial (re-visit them!); deduction for non-compliance: _____% (you choose as a group) on the final mark for this assignment

☐ be present in the paper feedback tutorial to participate as a group in the giving and receiving of the feedback; deduction for non-compliance: 10% on the final mark for this assignment

☐ give critical feedback in a polite way

☐ receive feedback graciously and without taking personal offense

☐ _____

☐ _____

I accept that by violating this contract I will face a decrease of my mark for this assignment ([composite] penalty specified above).

Group member 1, signature: _____

Group member 2, signature: _____

Group member 3, signature: _____

Group member 4, signature: _____

2. PPT presentation

You will be required to present a PPT talk to the class based on one primary literature paper, thus a scientific study (i.e. not a review). Topics cover extrinsic and intrinsic postzygotic isolation for the presentation session I (March 28) and polyploidy & hybrid speciation, reinforcement and adaptive radiation for the presentation session II (April 4). Half of the class will present during session I and the other half during session II. Please find a list of suggested papers below. You must sign up for a paper

and, hence, presentation date by March 14 by sending an email of your top three choices to Ivana Stehlik and topics will be allocated on a first-come-first-served basis. You may choose your own paper compatible with topics covered in class, i.e. papers other than those listed below if you prefer, but these must be approved by Ivana Stehlik. On the PPT presentation day, bring a memory stick with your file on it to upload onto the course laptop. If you are a mac user, convert your ppt presentation into a pdf to avoid file incompatibility (please note that fancy fly-ins [which should be avoided anyway] will not appear in basic pdf copies, thus make sure all you want to show in your Mac ppt copy will show in your pdf copy) .

Presentation goals

Presentations should be approximately 10 min long, and should fulfill three main goals:
(1) Bring the whole class 'up to speed' on the hypotheses, procedures and conclusions of the study. In order to do this, you will need to fill in background information which is unlikely to be common student knowledge. This may require consulting sources other than just your chosen paper.
(2) Highlight where the paper links to theory and general principals of evolutionary biology and the field of speciation.
(3) Answer potential audience questions.

Your duty as a member of an active audience

As an active audience member during a presentation, you cannot just take a nap… The role of the audience is to provide an attentive, receptive, but critical response to the material presented. Each student will be allocated a specific role to provide feedback, e.g. on the construction of the presentation or logical flow, slide quality and layout, on oral presentation skills, or on non-verbal communication.

Potential topics for presentations; session I (March 28; *plant paper; #animal paper)

- **Extrinsic postzygotic isolation:**

  #- Kuwajima M., Kobayashi N. and Katakura H. 2010. Detection of ecological hybrid inviability in a pair of sympatric phytophagous ladybird beetles (*Henosepilachna* spp.). Entomologia Experimentalis et Applicata 134: 280-286.

  *- Leotard G., Saltmarsh A., Kjellberg F. and Mckey D. 2008. Mutualism, hybrid inviability and speciation in a tropical ant-plant. Journal of Evolutionary Biology 21: 1133-1143.

  #- Veen T., Svedin N., Forsman J.T., Hjernquist M.B., Qvarnstrom A., Hjernquist K.A.T., Traff J. and Klaassen M. 2007. Does migration of hybrids contribute to post-zygotic isolation in flycatchers? Proceedings of the Royal Society B 274: 707-712.

- **Intrinsic postzygotic isolation:**

  #-Bono J.M. and Markow T.A. 2009. Post-zygotic isolation in cactophilic *Drosophila*: larval viability and adult life-history traits of *D-mojavensis*/*D-arizonae* hybrids. Journal of Evolutionary Biology 22: 1387-1395.

  #- Bronson c.L., Grubb T.C., Sattler G.D. and Braun M.J. 2005. Reproductive success across the black-capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) hybrid zone in Ohio. AUK 122: 759-772.

  *-Brothers A.N. and Delph L.F. 2010. Haldane's rule is extended to plants with sex chromosomes. Evolution 64: 3643-3648.

#-Christianson S.J., Swallow J.G. and Wilkinson G.S. 2005. Rapid evolution of postzygotic reproductive isolation in stalk-eyed flies. Evolution 59: 849-857.

#- Lijtmaer D.A., Mahler B. and Tubaro P.L. 2003. Hybridization and postzygotic isolation patterns in pigeons and doves. Evolution 57: 1411-1418.

#- Matute D.R. and Coyne J.A. 2010. Intrinsic reproductive isolation between two sister species of *Drosophila*. Evolution 64: 903-920.

#- Presgraves D.C. 2002. Patterns of postzygotic isolation in Lepidoptera. Evolution 56: 1168-1183.

#-Pryke S. R. and Griffith S.C. 2009. Postzygotic genetic incompatibility between sympatric color morphs. Evolution 63: 793-798.

*- Scopece G., Widmer A. and Cozzolino S. 2008. Evolution of postzygotic reproductive isolation in a guild of deceptive orchids. American Naturalist 171: 315-326.

#- Takahashi H., Nagai T. and Goto A. 2005. Hybrid male sterility between the fresh- and brackish-water types of ninespine stickelback *Pungitius pungitius* (Pisces, Gasterodeidae). Zoological Science 22: 35-40.

#- Tech C. 2006. Postzygotic incompatibilities between the pupfishes, *Cyprinodon elegans* and *Cyprinodon variegatus*: hybrid sterility and sex ratio bias. Journal of Evolutionary Biology 19: 1830-1837.

Potential topics for presentations; session II (April 4; *plant paper; #animal paper)

- **Polyploid and hybrid speciation:**

*- Cook L.M., Soltis P.S., Brunsfeld S.J. and Soltis D.E. 1998. Multiple independent formations of *Tragopogon* tetraploids (Asteraceae): evidence from RAPD markers. Molecular Ecology 7: 1293-1302.

*-Perrie L.R., Shepherd L.D., De Lange P.J. and Brownsey P.J. 2010. Parallel polyploid speciation: distinct sympatric gene-pools of recurrently derived allo-octoploid *Asplenium* ferns. Molecular Ecology 19: 2916-2932.

#- Ptacek M.B., Gerhardt H.C. and Sage R.D. 1994. Multiple origins of the tetraploid, *Hyla versicolor*. Evolution 48: 898-908.

*- Slotte T., Huang H.R., Lascoux M. ad Ceplitis A. 2008. Polyploid speciation did not confer instant reproductive isolation in *Capsella* (Brassicaceae). Molecular Biology and Evolution 25: 1472-1481.

*- Ramsey J. 2007. Unreduced gametes and neopolyploids in natural populations of *Achillea borealis* (Asteraceae). Heredity 98: 143-150.

- **Reinforcement:**

#-Cooley J.R., Simon c. and Marshall D.C. 2003. Temporal separation and speciation in periodical cicadas. BioScience 53: 151-157.

#- Hoskin C.J., Higgie M., McDonald K.R. and Moritz C. 2005. Reinforcement drives rapid allopatric speciation. Nature 437: 1353-1356.

#-Kameda Y., Kawakita A. and Makoto K. 2009. Reproductive character displacement in genital morphology in Satsuma land snails. American Naturalist 173: 689-697.

*-Kay and Schemske. 2008. Natural selection reinforces speciation in a radiation of neotropical rainforest plants. Evolution 62: 2628-2642.

#-Lemmon E.M. and Lemmon A.R. 2010. Reinforcement in chorus frogs: lifetime fitness estimates including intrinsic natural selection and sexual selection against hybrids. Evolution 64: 1748-1761.

#-Mullen s.P. and Andres J.A. 2007. Rapid evolution of sexual signals in sympatric Calopteryx damselflies: reinforcement or 'noisy-neighbour' ecological character displacement? Journal of Evolutionary Biology 20: 1637-1648.
*-Yost J.M. and Kay K.M. 2009. The evolution of postpollination reproductive isolation in *Costus*. Sexual Plant Reproduction 22: 247-255.

- **Adaptive radiation:**

*-Agrawal A.A., Fishbein M., Halitschke R., Hastings A.P., Rabosky D.L. and Rasmann S. 2009. Evidence for adaptive radiation from a phylogenetic study of plant defenses. Proceedings of the National Academy of Sciences of the United States 106: 18067-18072.
#-Givnish T.J., Millam K.C., Mast A.R., Paterson T.B., Theim T.J., Hipp A.L., Henss J.M., Smith J.F., Wood K.R. and Sytsma K.J. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). Proceedings of the Royal Society B 276: 407-416.
#-Joy J.B. and Crespi B.J. 2007. Adaptive radiation of gall-inducing insects within a single host-plant species. Evolution 61: 784-795.
#-Lengyel S., Gove A.D., Latimer A.M., Majer J.D., Dunn R.R. 2009. Ants sow the seeds of global diversification in flowering plants. PLoS ONE 4: e5480.
#-Losos J.B., Warheit K.I. and Schoener T.W. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70-73.
#-Matschiner M., Hanel R. and Salzburger W. 2011. On the origin and trigger of the notothenioid adaptive radiation. PLOS One 6: e18911.
#-von Rintelen K, Glaubrecht M. Schubart C.D., Wessel A. and von Rintelen T. 2010. Adaptive radiation and ecological diversification of Sulawesi's ancient lake shrimps. Evolution 64: 3278-3299.