

**Figure 1: Example of Ecological Niche Modeling (courtesy of T. Nakazato)**

lab for wild tomato species (Nakazato et al., *in review*) and in my own research with wild hamsters (unpub. manuscript). I will also quantify two axes of biotic ecological differentiation: 1) floral characteristics (e.g. color, stigma exertion, nectar guides) that correlate with shifts in pollinator or mating system; and 2) habitat characteristics (e.g. open versus shaded) indicative of competitive environment. While some of these data may gathered from online records, more detailed measurements (e.g. flower size) require “hands-on” manipulation.

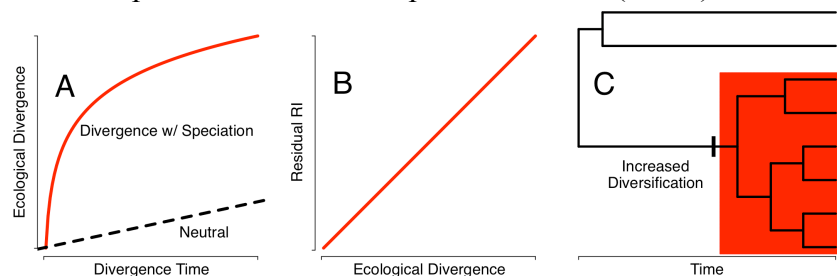
**Objective 2: Do ecological differences accumulate early in speciation?** - Ecological divergence will increase with time, but if ecological divergence causes speciation, then even young sister species should show niche differences comparable to that of older species. I will simulate phylogenies with ecological divergence accumulating randomly (e.g. Brownian motion) to generate neutral expectations. I will then regress ecological divergence, quantified using niche modeling, against divergence time using phylogenetically independent contrasts to test the hypothesis that ecological divergence causes speciation (Fig. 2a). I will further examine the correlation between ecological divergence and divergence time for each ecological axis (e.g. temperature) separately. Rather than testing a specific hypothesis, these analyses will be useful for generating candidate speciation traits that may be evaluated using experimentally and genetically tractable species such as wild and domesticated tomato (*Solanum* spp., Moyle, *in review*).

modeling, against divergence time using phylogenetically independent contrasts to test the hypothesis that ecological divergence causes speciation (Fig. 2a). I will further examine the correlation between ecological divergence and divergence time for each ecological axis (e.g. temperature) separately. Rather than testing a specific hypothesis, these analyses will be useful for generating candidate speciation traits that may be evaluated using experimentally and genetically tractable species such as wild and domesticated tomato (*Solanum* spp., Moyle, *in review*).

**Objective 3: Do other forms of RI arise as a byproduct of ecological divergence?** - Ecological speciation predicts that any form of RI can arise as a byproduct of ecological divergence (Fig. 2b). Funk et al. (11) found a positive relationship between a crude measure of ecological divergence and multiple forms of RI, after accounting for divergence time. I will perform a similar analysis using the more rigorous niche modeling approach described above along with crossing data from numerous *Solanum* species. I am currently in the process of collecting all the literature on crosses in *Solanum* and associated assays of RI (i.e. hybrid sterility/inviability).

Ecological speciation predicts that any form of RI can arise as a byproduct of ecological divergence (Fig. 2b). Funk et al. (11) found a positive relationship between a crude measure of ecological divergence and multiple forms of RI, after accounting for divergence time. I will perform a similar analysis using the more rigorous niche modeling approach described above along with crossing data from numerous *Solanum* species. I am currently in the process of collecting all the literature on crosses in *Solanum* and associated assays of RI (i.e. hybrid sterility/inviability).

**Objective 4: Diversification rate shifts** - An independent line of evidence for the role of ecological divergence in speciation is increased diversification rates associated with increased ecological opportunity (Fig. 2c). For example, several authors have implicated the importance of new niches formed during the Andean uplift as a cause of adaptive radiations (15-17). I will use BEAST (18) to estimate divergence times and SymmeTREE (19) to infer rate shifts associated with the Andean orogeny. The advantage of SymmeTREE is that it uses both branch length and topological information, and can



**Figure 2: Expected results from Objectives 2 (A), 3 (B), and 4 (C).**

accommodate incompletely resolved trees. Others in the Moyle lab have used a different approach to show that Andean uplift promoted speciation in wild tomato species (Nakazato et al., *in review*).

### *Anticipated Outcomes, Broader Impact, and Schedule*

This portion of my dissertation research employs rigorous ecological and phylogenetic methods to address a fundamental evolutionary question: does ecological divergence generally cause speciation? The proposed research is consistent with the Society for Systematic Biologists' aim of using systematic information to infer evolutionary pattern and process. I will use the results from these analyses to inform ongoing and future projects looking at the genetics of adaptation and speciation in *Solanum* via genomic screens of positive selection and QTL studies. Direct collaboration with expert *Solanum* systematists is essential for this project, both for accessing herbarium specimens and ensuring appropriate phylogenetic inference. Furthermore, work at the Natural History Museum will deepen my knowledge of *Solanum* biology and expand the impact of the PBI *Solanum* Project in a novel direction.

In the immediate future, I will 1) continue to synthesize crossing data in *Solanum* for use in Objective 3; 2) develop neutral phylogenetic simulations; and 3) coordinate with investigators from the PBI *Solanum* Project to access herbarium specimens. I will travel to the Natural History Museum during winter of my second year (2008-09) to collect data and analyze it for publication later in 2009. I will use the results from these analyses as part of an NSF Doctoral Dissertation Improvement Grant application in 2010.

1. J. A. Coyne, H. A. Orr, *Speciation* (Sinauer Associates, Sunderland, MA, 2004).
2. C. Darwin, *On the Origin of Species by Means of Natural Selection or the Preservation of Favored Races in the Struggle for Life* (J. Murray, London, 1859).
3. T. Dobzhansky, *Genetics and the Origin of Species* (Columbia University Press, New York, 1937).
4. D. Schluter, *The Ecology of Adaptive Radiation* (Oxford University Press, Oxford, U.K., 2000).
5. T. Price, *Speciation in Birds* (Roberts and Company, Greenwood Village, CO, 2007).
6. T. M. Panhuis, R. Butlin, M. Zuk, T. Tregenza, *Trends in Ecology & Evolution* **16**, 364 (2001).
7. W. R. Rice, in *Endless Forms: Species and Speciation* D. J. Howard, S. H. Berlocher, Eds. (Oxford University Press, New York, 1998).
8. M. J. D. White, *Modes of Speciation* (W. H. Freeman and Company, San Francisco, CA, 1978).
9. M. Lynch, A. G. Force, *American Naturalist* **156**, 590 (Dec, 2000).
10. D. Schluter, *Trends in Ecology & Evolution* **16**, 372 (Jul, 2001).
11. D. J. Funk, P. Nosil, W. J. Etges, *Proceedings of the National Academy of Sciences of the United States of America* **103**, 3209 (Feb, 2006).
12. PBI *Solanum* Project. Solanaceae Source <http://www.nhm.ac.uk/research-curation/projects/solanaceaesource/> (2008).
13. M. Nee, in *Solanaceae IV: Advances in Biology and Utilization* M. Nee, D. E. Symon, R. N. Lester, J. P. Jessop, Eds. (Royal Botanical Gardens, Kew, 1999) pp. 285-333.
14. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, *Int J Climatol* **25**, 1965 (2005).
15. J. E. Richardson, R. T. Pennington, T. D. Pennington, P. M. Hollingsworth, *Science* **293**, 2242 (Sep, 2001).
16. K. M. Kay, P. A. Reeves, R. G. Olmstead, D. W. Schemske, *American Journal of Botany* **92**, 1899 (2005).
17. C. Hughes, R. Eastwood, *Proceedings of the National Academy of Sciences of the United States of America* **103**, 10334 (2006).
18. A. Drummond, A. Rambaut, *BMC Evolutionary Biology* **7**, 214 (2007).
19. K. M. A. Chan, B. R. Moore, *Bioinformatics* **21**, 1709 (Apr, 2005).

*Budget Justification*

I will fly roundtrip from Indiana to London and stay for approximately one month. While \$35/day is not a sufficient stipend for London, the IU Graduate School offers matching funds that will cover additional costs.

Roundtrip flight to London - \$1000

One month living stipend - \$35 per diem x 30 days = \$1050

Total - \$2000