

# Luke Harmon

## *Curriculum Vitae*

### **Academic employment:**

- 2007 – present      Assistant Professor  
Department of Biological Sciences  
Adjunct, Department of Statistics  
Affiliated faculty, Bioinformatics and Computational Biology  
University of Idaho, Moscow, Idaho
- 2005-2007            Postdoctoral Fellow, Biodiversity Research Centre  
University of British Columbia, Vancouver, B.C.  
Supervisor: Dr. Dolph Schluter

### **Education:**

- 2000-2005            Washington University, St. Louis, MO  
Ph. D. in Evolution, Ecology, and Population Biology  
Advisor: Dr. Jonathan Losos
- 1994-1998            Iowa State University, Ames, IA  
B.S. with honors, summa cum laude  
Major: Zoology    Minor: Mathematics

### **Teaching experience:**

- 2010-2012            Lecturer, Biology 213 (Principles of Biological Structure and Function),  
University of Idaho
- 2009-2012            Seminar leader, Macroevolution, University of Idaho and  
Washington State University
- 2007-2012            Lecturer, Biology 489 (Herpetology), University of Idaho
- 2009                    Lecturer, Systematics, University of Idaho (co-taught with Jack Sullivan)
- 2007-2008            Co-instructor (with M. Alfaro), Macroevolution, University of Idaho and  
Washington State University
- 2006                    Lecturer, Biology 300 (Biometry), University of British Columbia
- 2001-2003            Teaching Assistant, Washington University (Ecology, Conservation Biology)
- 1999-2000            Head of Science, and Science Teacher for Forms 4 and 5  
Sir Dudley Tuti College, Ysabel Province, Solomon Islands, South Pacific
- 1995-1996            Leader and Seminar Coordinator, Freshman Honors Program  
Iowa State University

### **Grants, fellowships, and awards:**

- 2012-2015            NSF DEB, “Collaborative Research: phyloFlow: Comparative Analysis  
Workflows for the Tree of Life” (co-PIs Robert Thacker, Chelsea Specht, Curtis  
Lisle, and Jorge Soberon; total \$4,659,556, Harmon lab budget \$914,286;  
pending final NSF budget cuts)
- 2011-2012            NSF BEACON, “The Genetic Architecture of Multidimensional Adaptation  
and Speciation” (co-PIs Jenny Boughman and Erica Rosenblum; total \$96,900,  
Harmon lab budget \$1,500)
- 2011-2012            NSF BEACON, “Mystery of Mysteries” (co-PIs Jenny Boughman, Rich Lenski,  
and Barrie Williams; total \$165,353, Harmon lab budget \$3,442)

2011-2012	NSF BEACON, “Long-term consequences of evolution in action examined over a phylogeny” (co-PI Joe Felsenstein; total \$132,794, Harmon lab budget \$65,306)
2011	Early-Career Faculty Award, University of Idaho
2009-2011	NIH COBRE Administrative Supplement, “Evolution of Antibiotic Resistance in Bacterial Biofilms” (co-PI Erica Rosenblum; total \$399,488, Harmon lab budget \$199,488)
2009-2012	NSF DEB, “Collaborative Research: Tempo and Mode of Diversification in Vertebrates” (co-PI Mike Alfaro; total \$720,204, Harmon lab budget \$462,704)
2009-2012	NSF DEB, “RUI: REVSYS: Integrative Systematics of Gekkotan Lizards - Phylogenetic Resolution, Taxonomic Revision, and Comparative Biology” (PIs: Bauer and Jackman; total \$909,212; Harmon lab subcontract: \$45,923)
2009-2010	NIH COBRE pilot grant, University of Idaho, \$39,726
2009	Short-term sabbatical award: Integrating Fossil and Molecular Data in the Study of Diversification, NESCent, Duke University, Durham, NC
2009	Young Investigators Prize, American Society of Naturalists
2008-2009	NIH COBRE pilot grant addendum, University of Idaho, \$22,500
2008-2009	NIH COBRE pilot grant, University of Idaho, \$39,720
2005-2007	Biodiversity Postdoctoral Fellowship, University of British Columbia
2006	Just Desserts Award (for services to graduate students), University of British Columbia
2002-2005	National Science Foundation Dissertation Improvement Grant, \$10,800
2001-2004	National Science Foundation Graduate Research Fellowship

#### **Student Grants:**

2011	Travis Hagey, Student Travel Grant, Univ. Idaho, \$490
2011	Simone Des Roches, Student Travel Grant, Univ. Idaho, \$514
2011	Brian Lohman, Biology Dept. Research Grant, Univ. Idaho, \$500
2011	Travis Hagey, SSAR Travel Award, \$400
2011	Travis Hagey, Student Travel Grant, Univ. Idaho, \$539
2010	Travis Hagey, IDEA Travel Grant, Univ. Idaho, \$1500
2010	Travis Hagey, American Society of Naturalists Travel Award, \$500
2010	Simone Des Roches, Student Grant Program, Univ. Idaho, \$2986
2010	Simone Des Roches, ASIH Gage Grant, \$500
2010	Matt Pennell, NSERC PGS-M, \$17200
2010	Simone Des Roches, NSERC PGS-D, \$63000
2009	Simone Des Roches, NSERC PGS-M, \$17200
2009	Simone Des Roches, Student Grant Program, Univ. Idaho, \$2888
2009	Simone Des Roches, Travel Grant, Univ. Idaho, \$800
2009	Jack Torresdal, Student Grant Program, Univ. Idaho, \$961
2009	Jack Torresdal, Berklund Undergraduate Research Award, Univ. Idaho, \$3000
2008	Travis Hagey, Student Grant Program, Univ. Idaho, \$1450
2006	Nick Smeenk, Biology Department Research Grant, Univ. Idaho, \$1431

#### **Activities:**

2012-present	Associate Editor, Evolution
2011-present	Associate Editor, Systematic Biology
2011-present	Associate Editor, Methods in Ecology and Evolution

2011	Coordinated course, Comparative Methods in R; Canadian Society for Ecology and Evolution Annual Meeting, Banff, Canada
2011	Keynote speaker, Zoological Society of London, “Integrating Ecology into Macroevolutionary Research”
2009	Invited speaker, symposium: Evolution 101: Evolution and Biogeography, at Evolution Meetings in Moscow, ID
2009	Invited speaker, symposium: Eco-evolutionary Dynamics - Should Ecologists Care? Ecological Society of America meetings in Albuquerque, NM.
2008	Co-coordinated (with M. Alfaro) and gave presentation in Late Breaking Symposium: Testing Macroevolutionary Hypotheses of Diversification: Approaches and Perspectives, at SICB meetings in San Antonio, TX.
2005-2006	Coordinator, Ecology and Evolution Retreat, University of British Columbia, University of Victoria, and Simon Fraser University
2005-2007	Coordinator, Biodiversity Discussion Group, University of British Columbia
2005	Seminar speaker, University of British Columbia
2002-present	Member, NCEAS Adaptive Radiation Working Group
Invited speaker:	2006: University of Victoria, Simon Fraser University, University of Calgary, University of Idaho, Rice University, University of Glasgow, Iowa State University; 2007: Harvard University, University of Washington, University of Idaho (Dept. of Agriculture), Washington State University (Anthropology); 2008: Lewis and Clark University, Washington State University (Biology); 2009: University of Ottawa, Duke University, University of Texas; 2010: University of California, Berkeley; 2011: University of Chicago, phyloseminar.org (online seminar); 2012 (planned): University of Colorado, University of Michigan, Michigan State University, University of Kansas, EAWAG (Switzerland)
Advising:	Four current doctoral students: T. Hagey, D. Jochimsen, S. Des Roches*, and M. Pennell (*coadvised with E. B. Rosenblum); two postdoctoral researchers, J. Eastman and J. Brown. Former lab members: J. Tyerman (postdoc) Student committees: <b>Completed</b> Chad Brock (WSU MSc, 2009), William Godsoe (UI PhD 2009), Jon Eastman (WSU PhD 2010), Barb Banbury (WSU PhD 2010), Hugo Alamillo (WSU PhD 2010); <b>In progress</b> Brice Sarver (UI), Cody Hinchliff (WSU), Kayla Hardwick (UI), Simon Uribe-Convers (UI)

### **Publications († indicates student coauthor):**

#### **In revision:**

Alfaro, M. E., L. J. Harmon, and J. P. Huelsenbeck. *In revision*. Does the no-common mechanism model perform well in the analysis of morphological data sets? For *Systematic Biology*.

Harmon, L. J. *In revision*. A nonparametric method to test for correlated evolution in a phylogenetic context. For *Systematic Biology*.

Banbury, B. A.†, L. J. Harmon, and M. E. Alfaro. Discordant evolutionary patterns of morphology and mechanics in complex traits. To be resubmitted to *Journal of Evolutionary Biology*.

Alamillo, H., C. D. Brock, L. J. Harmon, and M. E. Alfaro. *In revision*. Red Queens, Court Jesters, and Snake Biodiversity: Tests of Ophidian Macroevolution. To be resubmitted to *Proc. Roy. Soc. B*.

Davies, T. J.\*, L. J. Harmon\*, and P. Goldblatt. *In revision*. Evolution of flower symmetry in Asterids and Irids: estimating evolutionary rates and ancestral states in sparsely sampled clades. To be resubmitted to *Evolution*.

Des Roches, S.<sup>†</sup>, L. J. Harmon, J. B. Shurin, and D. Schluter. *In revision*. Ecological and evolutionary effects of stickleback on ecosystem function.

Davis, C. C., H. Schaefer, W. R. Anderson, Z. Xi, D. A. Baum, M. J. Donoghue, and L. J. Harmon. *In revision*. Long-term morphological stasis maintained by a plant-pollinator mutualism.

Pennell, M. W., B. A. J. Sarver, and L. J. Harmon. *In revision*. Trees of Unusual Size: Sampling Bias Can Influence Inference of Early Bursts from Molecular Phylogenies.

#### **In review:**

Wagner, C. E., L. J. Harmon, and O. Seehausen. Ecological opportunity and sexual selection together predict adaptive radiation. Submitted to *Nature*, 17 January 2012.

Rosindell, J. and L. J. Harmon. *In review*. A unified model of species immigration, extinction and abundance on islands. Submitted to *Journal of Biogeography*, 5 December 2011.

#### **Peer reviewed papers, published or in press**

Rosenblum, E. B.\*, B. A. J. Sarver, J. W. Brown, S. Des Roches, K. M. Hardwick, T. D. Hether, J. M. Eastman, M. W. Pennell, and L. J. Harmon\*. Accepted pending revisions. Goldilocks meets Santa Rosalia: An ephemeral speciation model explains patterns of diversification across time scales. *Evolutionary Biology*.

Rosindell, J., S. P. Hubbell, F. He, L. J. Harmon, and R. S. Etienne. *In press*. Drift happens: A case for ecological neutral theory. *Trends in Ecology and Evolution*.

Godsoe, W. and L. J. Harmon. *In press*. How do species interactions affect species distribution models? *Ecography*.

Slater, G. J., L. J. Harmon, P. Joyce, L. J. Revell, and M. E. Alfaro. *In press*. Fitting models of continuous trait evolution to incompletely sampled comparative data using Approximate Bayesian Computation. *Evolution*, online early.

Stack, J., L. J. Harmon, and B. O'Meara. 2011. RBrownie: An R package for testing hypotheses about rates of evolutionary change. *Methods in Ecology and Evolution* 2: 660-662.

Eastman, J. M., M. E. Alfaro, P. Joyce, A. L. Hipp, and L. J. Harmon. 2011. A novel comparative method for modeling shifts in the rate of character evolution on trees. *Evolution* 65: 3578-3589.

Eastman, J. M., L. J. Harmon, H.-J. La, P. Joyce, and L. J. Forney. 2011. The onion model, a simple neutral model for the evolution of diversity in bacterial biofilms. *J. Evol. Biol.* 11: 2496-2504.

Des Roches, S., J. M. Robertson, L. J. Harmon, and E. B. Rosenblum. 2011. Ecological release in white sands lizards. *Ecology and Evolution* 1: 571-578.

Davies, T. J., G. Smith, D. U. Bellstedt, J. Boatwright, B. Bytebier, R. Cowling, F. Forest, L. J. Harmon, A. M. Muasya, B. D. Schrire, Y. Steenkamp, M. van de Bank, and V. Savolainen. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biology* 9: e1000620.

Smith, K. L.<sup>†</sup>, L. J. Harmon, L. Shoo<sup>†</sup>, and J. Melville. 2011. Evidence of constrained phenotypic evolution in a cryptic species complex of agamid lizards. *Evolution* 65: 976-992.

Brock, C. D.<sup>†</sup>, L. J. Harmon, and M. E. Alfaro. 2011. Testing for Temporal Variation in Diversification Rates When Sampling is Incomplete and Nonrandom. *Systematic Biology* 60: 410-419.

Carlson, B. A., S. M. Hasan, M. Hollmann, D. B. Miller, L. J. Harmon, and M. E. Arnegard. 2011. Brain evolution triggers explosive diversification of species and signals. *Science* 332: 583-586.

Rosenblum, E. B. and L. J. Harmon. 2011. Same same but different: replicated ecological speciation at White Sands. *Evolution* 65: 946-960.

Arnegard, M. E., P. B. McIntyre, L. J. Harmon, M. L. Zelditch, W. G. R. Crampton, J. K. Davis, J. P. Sullivan, S. Lavoué, and C. D. Hopkins. 2010. Sexual signal evolution outpaces ecological divergence during electric fish species radiation. *American Naturalist* 176:335-356.

Yoder, J. B.<sup>†</sup>, S. Des Roches<sup>†</sup>, J. M. Eastman<sup>†</sup>, L. Gentry<sup>†</sup>, W. K. W. Godsoe, T. Hagey<sup>†</sup>, D. Jochimsen<sup>†</sup>, B. P. Oswald<sup>†</sup>, J. Robertson, B. A. J. Sarver<sup>†</sup>, J. J. Schenk<sup>†</sup>, S. F. Spear<sup>†</sup>, and L. J. Harmon. 2010. Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology* 23: 1581-1596, doi:10.1111/j.1420-9101.2010.02029.x.

Harmon, L. J., J. B. Losos, J. Davies, R. G. Gillespie, J. L. Gittleman, W. B. Jennings, K. Kozak, M. A. McPeck, F. Moreno-Roark<sup>†</sup>, T. J. Near, A. Purvis, R. E. Ricklefs, D. Schluter, J. A. Schulte II, O. Seehausen, B. Sidlauskas, O. Torres-Carvajal<sup>†</sup>, J. T. Weir<sup>†</sup>, & A. Ø. Mooers. 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64: 2385-2396. doi:10.1111/j.1558-5646.2010.01025.x.

Harmon, L. J. and R. E. Glor. 2010. Poor statistical performance of the Mantel test in phylogenetic comparative analyses. *Evolution* 64: 2173-2178, doi:10.1111/j.1558-5646.2010.00973.x.

Matthews, B., L. J. Harmon, L. M'Gonigle<sup>†</sup>, K. B. Marchinko<sup>†</sup>, and H. Schaschl. 2010. Sympatric and allopatric divergence of MHC genes in threespine stickleback. *PLoS ONE* 5:e10948.

Hagey, T. J.<sup>†</sup>, J. B. Losos, and L. J. Harmon. 2010. Cruise foraging of invasive chameleons (*Chamaeleo jacksonii*) in Hawaii. *Breviora* 519:1-7.

Alfaro, M. E., F. Santini, C. Brock<sup>†</sup>, H. Alamillo<sup>†</sup>, A. Dornburg<sup>†</sup>, D. L. Rabosky<sup>†</sup>, G. Carnevale, and L. J. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *PNAS* 106:13410-13414.

Santini, F., L. J. Harmon, G. Carnevale, and M. E. Alfaro. 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evolutionary Biology* 9: 194.

Ingram, T.<sup>†</sup>, L. J. Harmon, and J. B. Shurin. 2009. Niche evolution, trophic structure and species turnover in model food webs. *American Naturalist* 174: 56-67.

Harmon, L. J.<sup>\*</sup>, B. Matthews<sup>\*</sup>, S. Des Roches<sup>†</sup>, J. Chase, J. Shurin, and D. Schluter. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458: 1167-1170.

Nosil, P., L. J. Harmon, and O. Seehausen. 2009. Ecological explanations for (incomplete) speciation. *Trends in Ecology and Evolution* 24:145-156.

Pinto, G.<sup>†</sup>, D. L. Mahler<sup>†</sup>, L. J. Harmon, and J. B. Losos. 2008. Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proceedings of the Royal Society B* 275: 2749-2757.

Revell, L. J.<sup>†</sup>, L. J. Harmon, and D. C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 57: 591-601.

Harmon, L. J., J. Melville, A. Larson, and J. B. Losos. 2008. The Role of Geography and Ecological Opportunity in the Diversification of Day Geckos (*Phelsuma*). *Systematic Biology* 57: 562-573.

Revell, L. J.<sup>†</sup> and L. J. Harmon. 2008. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* 10: 311-321.

Harmon, L. J., J. Weir<sup>†</sup>, C. Brock<sup>†</sup>, R. E. Glor, and W. Challenger<sup>†</sup>. 2008. GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24:129-131.

Harmon, L. J., L. L. Harmon, and C. G. Jones. 2007. Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean. *Oikos* 116: 1863-1878, DOI: 10.1111/j.2007.0030-1299.15958.x.

Vellend, M., L. J. Harmon, J. L. Lockwood, M. M. Mayfield, A. R. Hughes, J. P. Wares, and D. F. Sax. 2007. Effects of exotic species on evolutionary diversification. *Trends in Ecology and Evolution* 22: 481-488.

Nicholson, K. E., L. J. Harmon, and J. B. Losos. 2007. Evolution of *Anolis* lizard dewlap diversity. *PLoS ONE* 2(3): e274. doi:10.1371/journal.pone.0000274.

Revell, L. J.<sup>†</sup>, L. J. Harmon, R. B. Langerhans, and J. J. Kolbe. 2007. A phylogenetic approach to determining the importance of constraint on phenotypic evolution in the neotropical lizard *Anolis cristatellus*. *Evolutionary Ecology Research* 9: 261-282.

Harmon, L. J. and R. Gibson. 2006. Multivariate phenotypic evolution among island and mainland populations of the ornate day gecko, *Phelsuma ornata*. *Evolution* 60: 2622-2632.

Melville, J., L. J. Harmon, and J. B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society Series B: Biological Sciences* 273: 557-563.

Harmon, L. J. and J. B. Losos. 2005. The effect of intraspecific sample size on type I and type II error rates in comparative studies. *Evolution* 59:2705-2710.

Revell, L. J., L. J. Harmon, and R. E. Glor, 2005. Under-parameterized model of sequence evolution leads to bias in the estimation of diversification rates from molecular phylogenies. *Systematic Biology* 54: 973-983.

Weisrock, D. W., L. J. Harmon, and A. Larson. 2005. Resolving deep phylogenetic relationships in salamanders: analyses of mitochondrial and nuclear genomic data. *Systematic Biology* 54:758-777.

Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, species coexistence, and diversification rates in dusky salamanders (Plethodontidae, Desmognathinae). *Evolution* 59: 2000-2016.

Harmon, L. J., K. Bauman, M. McCloud, J. Parks, S. Howell, and J. B. Losos. 2005. What the free-ranging animals do at the zoo: a study of the behavior and habitat use of opossums (*Didelphis virginiana*) on the grounds of the St. Louis Zoo. *Zoo Biology* 24: 197-213.

Harmon, L. J., J. J. Kolbe, J. M. Cheverud, and J. B. Losos. 2005. Convergence and the multidimensional niche. *Evolution* 59: 409-421.

Harmon, L. J., J. A. Schulte, J. B. Losos, and A. Larson. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301: 961-964.

Harmon, L. J. 2002. Some observations of the natural history of the prehensile-tailed skink, *Corucia zebrata*, in the Solomon Islands. *Herpetological Review* 33: 177-179.

Harmon, L. J. 2000. A Translocation Strategy for Confiscated Pancake Tortoises. *Chelonian Conservation and Biology* 3(4):738-743.

Kolbe, J. J., L. J. Harmon, and D. A. Warner. 1999. New state record lengths and associated natural history notes for some Illinois snakes. *Transactions of the Illinois State Academy of Science* 92:133-135.

### **Book Chapters and Other Publications**

Harmon, L. J. In press. Macroevolutionary rates. In: J. B. Losos, *Ed.*, The Princeton Guide to Evolution. Princeton University Press.

McInnes, L., W. J. Baker, T. G. Barraclough, K. K. Dasmahapatra, A. Goswami, L. J. Harmon, H. Morlon, A. Purvis, J. Rosindell, G. H. Thomas, S. T. Turvey, and A. B. Phillimore. 2011. Integrating ecology into macroevolutionary research (meeting report). *Biology Letters* 7: 644-646.

Harmon, L. J. 2011. My island life. In: J. B. Losos, editor. *Evolution Emerging: Essays from Leading Evolutionary Biologists*. Roberts & Company Publishers.

Harmon, L. J. 2010. Journal Club: An evolutionary biologist ponders the pace of evolution. *Nature* 463: 1003.

Harmon, L. J. and S. Braude. 2010. Conservation of Small Populations: Effective Population Size, Inbreeding, and the 50/500 Rule. pp. 125-138 *in* S. Braude and B. S. Low, *Eds.*, An Introduction to Methods and Models in Ecology and Conservation Biology. Princeton University Press.

Bailey, J. K., A. Hendry, M. Kennison, D. Post, E. Palkovacs, F. Pelletier, L. J. Harmon, and J. A. Schweitzer. 2009. From Genes to Ecosystems: An Emerging Synthesis of Eco-Evolutionary Dynamics. *New Phytologist* 184: 746–749.

Nosil, P. and L. J. Harmon. 2009. Niche dimensionality and ecological speciation. In: R. Butlin, J. Bridle, and D. Schluter, editors. *Speciation and Patterns of Diversity*. Cambridge University Press.

Mooers, A.O., Harmon, L.J., Wong, D.H.J., and S.B. Heard. 2007. Some models of phylogenetic tree shape. Pages 147-168 *in* New Mathematical Models for Evolution (O. Gascuel and M. Steel, eds.), Oxford University Press, Oxford.

\* Order of authorship is arbitrary

#### **References:**

Dr. Jack Sullivan  
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