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## Ryan A. Chisholm

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### EDUCATION

**Princeton University**, Princeton, New Jersey, USA

- Ph.D., Ecology and Evolutionary Biology, Advisor: Simon Levin 2010
- M.A., Ecology and Evolutionary Biology 2007

**University of Melbourne**, Melbourne, Australia

- B.Sc., Mathematics and Statistics (Honours in Botany), Advisor: Mark Burgman 2001 (2004)
  - B.A., German 2001
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### APPOINTMENTS

**National University of Singapore**, Singapore

- Associate Professor, Department of Biological Sciences 2019–
- Assistant Professor, Department of Biological Sciences 2012–2018

**Smithsonian Tropical Research Institute**, Panama

- Post-doctoral researcher: “Tropical Forest Dynamics and Global Change” 2010–2012
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### TEACHING EXPERIENCE

**National University of Singapore**, Singapore

- Course co-designer and co-lecturer: *Evolutionary Biology* (first-year undergraduate course) 2016–present
  - Course designer and lecturer: *Methods in Mathematical Biology* (fourth-year undergraduate course) 2014–present
  - Course designer and lecturer: *Theoretical Biology* (graduate course) 2013–present
- 

### AWARDS, FELLOWSHIPS AND GRANTS

- Singapore Ministry of Education Reimagine grant: Mechanistic epidemiological modelling of dengue in Singapore 2021–2024
- Singapore Ministry of Education Tier 1 grant: Evolutionary game theory models to predict conservation outcomes 2021–2024
- National University of Singapore Faculty of Science Teaching Excellence Award 2019
- National Research Foundation of Singapore–Israel Science Foundation Joint Grant: A unified framework for stochastic ecological models of plant communities driven by temporal environmental stochasticity 2018–2021
- James S. McDonnell Foundation Studying Complex Systems Scholar Award: Modeling complex ecological communities: From small islands to tropical forests 2016–2021
- Singapore Ministry of Education Tier 1 grant: Quantifying undetected extinctions in an era of global change 2016–2018

- National University of Singapore Faculty of Science Young Scientist Award 2014
- Singapore Ministry of Education Tier 1 grant: Effect of spatial patterns of habitat loss on species loss in Southeast Asia 2013–2016
- National University of Singapore Faculty of Science start-up grant: Tropical forest dynamics and global change 2012–2015
- National University of Singapore Department of Biological Sciences start-up grant: Environmental drivers of tropical tree community dynamics 2012–2015
- Center for Tropical Forest Science – Smithsonian Institution Global Earth Observatories Postdoctoral Fellowship 2010–2012
- Award for Outstanding Teaching by a Graduate Student, Department of Ecology and Evolutionary Biology, Princeton University 2009
- Africa Grand Challenge Research Grant 2008–2009
- David Gardner '69 Research Grant 2008–2009
- Robert May Fellowship, Princeton University 2005–2006
- Bruce Knox Honours Prize, University of Melbourne 2004

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## PUBLICATIONS

*Peer reviewed*

- Davies, S. J., and 156 coauthors including **R. A. Chisholm**. 2021. ForestGEO: Understanding forest diversity and dynamics through a global observatory network. *Biological Conservation* 253:108907
- **Chisholm, R. A.**, and T. Swinfield. 2020. Automated Vegetation Monitoring for Forest Restoration. In S. Elliott, G. Gale, and M. Robertson (editors), *Automated Forest Restoration: Could Robots Revive Rain Forests?* FORRU-CMU
- Hülsmann, L., **R. A. Chisholm**, and F. Hartig. 2021. Is variation in conspecific negative density dependence driving tree diversity patterns at large scales? *Trends in Ecology and Evolution* (in press)
- Thompson, S. E. D., **R. A. Chisholm**, and J. Rosindell. 2020. `pycoalescence` and `rcoalescence`: packages for simulating spatially explicit neutral models of biodiversity. *Methods in Ecology and Evolution* 11:1237-1246
- **Chisholm, R. A.** and T. Fung. 2020. Janzen–Connell effects are a weak impediment to competitive exclusion. *The American Naturalist* 196:649–661
- Rosindell, J., and **R. A. Chisholm**. 2020. The Species–Area Relationships of Ecological Neutral Theory. In T. J. Matthews, K. A. Triantis, and R. J. Whittaker (editors), *The Species–Area Relationship: Theory and Application*, Cambridge University Press (in press)
- Pande, J., T. Fung, **R. A. Chisholm**, and N. Shnerb. 2020. Invader growth rate and its relevance to persistence and invasibility: a response to Technical Comment by Ellner *et al.* *Ecology Letters* 23:1725–1726
- Lum, D. W. H., P. A. Tedesco, B. Hugueny, X. Giam, and **R. A. Chisholm**. 2020. Quantifying the relative performance of two undetected-extinction models. *Conservation Biology* 35:239–248
- Kristensen, N. P., W. W. Seah, K. Y. Chong, Y. S. Yeoh, T. Fung, L. M. Berman, H. Z. Tan, and **R. A. Chisholm**. 2020. Extinction rate of discovered and undiscovered plants in Singapore. *Conservation Biology* 34:1229–1240

- Teo, A., N. P. Kristensen, J. A. Keuskamp, T. A. Evans, M. Foo, and **R. A. Chisholm**. 2020. Validation and extension of the tea bag index to collect decomposition data from termite-rich ecosystems. *Pedobiologia* 80:150639
- Theng, M., W. F. A. Jusoh, A. Jain, B. Huertas, D. J. X. Tan, H. Z. Tan, N. P. Kristensen, R. Meier, and **R. A. Chisholm**. 2020. A comprehensive assessment of diversity loss in a well-documented tropical insect fauna: Almost half of Singapore’s butterfly species extirpated in 160 years. *Biological Conservation* 242:108401
- Pande, J., T. Fung, **R. A. Chisholm**, and N. Shnerb. 2020. Mean growth rate when rare is not a reliable metric for persistence of species. *Ecology Letters* 23:274–282
- Fung, T., S. Verma, and **R. A. Chisholm**. 2020. Probability distributions of extinction times, species richness, and immigration and extinction rates in neutral ecological models. *Journal of Theoretical Biology* 485:110051
- Lam, W. N., and **R. A. Chisholm**. 2020. Resource conversion: a generalizable mechanism for resource-mediated positive species interactions. *Oikos* 129:209–223
- Fung, T., **R. A. Chisholm**, K. Anderson-Teixeira, N. Bourg, W. Y. Brockelman, S. Bunyavejchewin, C.-H. Chang-Yang, R. Chitra-Tarak, G. Chuyong, R. Condit, H. S. Dattaraja, S. J. Davies, C. E. N. Ewango, G. Fewless, C. Fletcher, C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, Z. Hao, J. A. Hogan, R. Howe, C.-F. Hsieh, D. Kenfack, Y. Lin, K. Ma, J.-R. Makana, S. McMahon, W. J. McShea, X. Mi, A. Nathalang, P. S. Ong, G. Parker, E.-P. Rau, J. Shue, S.-H. Su, R. Sukumar, I.-F. Sun, H. S. Suresh, S. Tan, D. Thomas, J. Thompson, R. Valencia, M. I. Vallejo, X. Wang, Y. Wang, P. Wijekoon, A. Wolf, S. Yap, and J. Zimmermann. 2020. Temporal population variability in local forest communities increases with latitude but has mixed effects on tree species richness. *Ecology Letters* 23:160–171
- Thompson, S. E. D., **R. A. Chisholm**, and J. Rosindell. 2019. Characterizing extinction debt following habitat fragmentation using neutral theory. *Ecology Letters* 22:2087–2096
- Menge, D. N. L., **R. A. Chisholm**, S. J. Davies, K. A. Salim, D. Allen, M. Alvarez, N. Bourg, W. Y. Brockelman, S. Bunyavejchewin, N. Butt, M. Cao, W. Chanthorn, W.-C. Chao, K. Clay, R. Condit, S. Cordell, J. Batista da Silva, H. S. Dattaraja, A. C. Segalin de Andrade, A. A. de Oliveira, J. den Ouden, M. Drescher, C. Fletcher, C. P. Giardina, C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, B. C. H. Hau, F. He, R. Howe, C.-F. Hsieh, S. P. Hubbell, F. M. Inman-Narahari, P. A. Jansen, D. J. Johnson, L. S. Kong, K. Král, C.-C. Ku, J. Lai, A. J. Larson, X. Li, Y. Li, L. Lin, Y. Lin, S. Liu, S. K. Y. Lum, J. A. Lutz, K. Ma, Y. Malhi, S. McMahon, W. McShea, X. Mi, M. Morecroft, J. A. Myers, A. Nathalang, V. Novotny, P. Ong, D. A. Orwig, R. Ostertag, G. Parker, R. P. Phillips, K. Abd. Rahman, K. Sack, W. Sang, G. Shen, A. Shringi, J. Shue, S.-H. Su, R. Sukumar, I.-F. Sun, H. S. Suresh, S. Tan, S. C. Thomas, P. S. Toko, R. Valencia, M. I. Vallejo, A. Vicentini, T. Vrška, B. Wang, X. Wang, G. D. Weiblen, A. Wolf, H. Xu, S. Yap, L. Zhu, and T. Fung. 2019. Patterns of nitrogen-fixing tree abundance in forests across Asia and America. *Journal of Ecology* 107:2598–2610
- Fung, T., S. Xiao, and **R. A. Chisholm**. 2019. Spatial scaling of species richness–productivity relationships for local communities: Analytical results from a neutral model. *Theoretical Ecology*
- Loke, L. H. L., **R. A. Chisholm**, and P. A. Todd. 2019. Effects of habitat area and spatial configuration on biodiversity in an experimental intertidal community. *Ecology* 100:e02757
- Fung, T., J. P. O’Dwyer, and **R. A. Chisholm**. 2019. Partitioning the effects of deterministic and stochastic processes on species extinction risk. *Ecological Complexity* 38:156–167
- Kristensen, N. P., **R. A. Chisholm**, and E. McDonald-Madden. 2019. Dealing with high uncertainty in qualitative network models using Boolean analysis. *Methods in Ecology and Evolution* 10:1048–1061
- Coleman, J., 134 coauthors including **R. A. Chisholm**, and L. R. Carrasco. 2019. One hundred top research questions for biodiversity conservation in Southeast Asia. *Biological Conservation* 234:211–220

- Kristensen, N. P., J. Johansson, **R. A. Chisholm**, H. G. Smith, and H. Kokko. 2018. Carryover effects from natal habitat type upon competitive ability lead to trait divergence or source–sink dynamics. *Ecology Letters* 21:1341–1352
- **Chisholm, R. A.**, F. Lim, Y. S. Yeoh, W. W. Seah, R. Condit, and J. Rosindell. 2018. Species–area relationships and biodiversity loss in fragmented landscapes. *Ecology Letters* 21:804–813
- **Chisholm, R. A.**, and T. Fung. 2018. Comment on “Plant diversity increases with the strength of negative density dependence at the global scale”. *Science* 360:eaar4685
- Belcher, R. N., and **R. A. Chisholm**. 2018. Tropical vegetation and residential property value: a hedonic pricing analysis in Singapore. *Ecological Economics* 149:149–159
- Fung, T., J. P. O’Dwyer, and **R. A. Chisholm**. 2018. Quantifying species extinction risk under temporal environmental variance. *Ecological Complexity* 34:139–146
- Lin, Y., L. Wijedasa, and **R. A. Chisholm**. 2017. Singapore’s willingness to pay for mitigation of transboundary forest-fire haze from Indonesia. *Environmental Research Letters* 12:024017
- Fung, T., J. P. O’Dwyer, and **R. A. Chisholm**. 2017. Species-abundance distributions under colored environmental noise. *Journal of Mathematical Biology* 74:289–311
- **Chisholm, R. A.**, T. Fung, D. Chimalakonda, and J. P. O’Dwyer. 2016. Maintenance of biodiversity on islands. *Proceedings of the Royal Society B* 283:20160102
- Fung, T., J. P. O’Dwyer, K. Abd. Rahman, C. D. Fletcher, and **R. A. Chisholm**. 2016. Reproducing static and dynamic biodiversity patterns in tropical forests: the critical role of environmental variance. *Ecology* 95:1207–1217
- **Chisholm, R. A.**, L. S. Wijedasa, and T. Swinfield. 2016. The need for long-term remedies for Indonesia’s forest fires. *Conservation Biology* 30:5–6
- **Chisholm, R. A.**, X. Giam, K. Sadanandan, T. Fung, and F. E. Rheindt. 2016. A robust non-parametric method for quantifying undetected extinctions. *Conservation Biology* 30:610–617
- Bourguignon T., **R. A. Chisholm**, and T. A. Evans. 2016. The termite ‘worker’ phenotype evolved as a dispersal strategy for fertile wingless individuals before eusociality. *The American Naturalist* 187:372–387
- **Chisholm, R. A.**, D. N. L. Menge, T. Fung, N. S. G. Williams, and S. A. Levin. 2015. The potential for alternative stable states in nutrient-enriched invaded grasslands. *Theoretical Ecology* 8:399–417
- Fung T., L. Villain, and **R. A. Chisholm**. 2015. Analytical formulae for computing dominance from species-abundance distributions. *Journal of Theoretical Biology* 386:147–158
- Bewick, S., **R. A. Chisholm**, E. Akçay, and W. Godsoe. 2015. A stochastic biodiversity model with overlapping niche structure. *Theoretical Ecology* 8:81–109
- O’Dwyer, J. P. and **R. A. Chisholm**. 2014. A mean field model for competition: from neutral ecology to the Red Queen. *Ecology Letters* 17:961–969
- **Chisholm, R. A.**, R. Condit, K. Abdul Rahman, P. J. Baker, S. Bunyavejchewin, Y.-Y. Chen, G. Chuyong, H. S. Dattaraja, S. Davies, C. E. N. Ewango, C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, S. P. Hubbell, D. Kenfack, S. Kiratiprayoon, Y. Lin, J.-R. Makana, N. Pongpattananurak, S. Pulla, R. Punchi-Manage, R. Sukumar, S.-H. Su, I.-F. Sun, H. S. Suresh, S. Tan, D. Thomas, and S. Yap. 2014. Temporal variability of forest communities: empirical estimates of population change in 4000 tree species. *Ecology Letters* 17:855–865
- **Chisholm, R. A.** and J. P. O’Dwyer. 2014. Species ages in neutral biodiversity models. *Theoretical Population Biology* 93:85–94

- Muller-Landau, H. C., M. Detto, **R. A. Chisholm**, and R. Condit. 2014. Detecting and predicting global change influences on forest biomass. In S. A. Coomes, D. F. R. P. Burslem, W. D. Simonson (editors), *Forests and Global Change*, British Ecological Society, 381–415
- **Chisholm, R. A.**, J. Cui, S. K. Y. Lum, and B. M. Chen. 2013. UAV LiDAR for below-canopy forest surveys. *Journal of Unmanned Vehicle Systems* 1:61–68
- Bai, F., **R. A. Chisholm**, W. Sang, and M. Dong. 2013. Spatial risk assessment of alien invasive plants in China. 2013. *Environmental Science and Technology*. 47:7624–7632
- **Chisholm, R. A.**, H. C. Muller-Landau, K. Abdul Rahman, D. P. Bebbler, Y. Bin, S. A. Bohlman, N. A. Bourg, J. Brinks, S. Bunyavejchewin, N. Butt, H. Cao, M. Cao, D. Cárdenas, L.-W. Chang, J.-M. Chiang, G. Chuyong, R. Condit, H. S. Dattaraja, S. Davies, A. Duque, C. Fletcher, N. Gunatilleke, S. Gunatilleke, Z. Hao, R. D. Harrison, R. Howe, C.-F. Hsieh, S. P. Hubbell, A. Itoh, D. Kenfack, S. Kiratiprayoon, A. J. Larson, J. Lian, D. Lin, H. Liu, J. A. Lutz, K. Ma, Y. Malhi, S. McMahon, W. McShea, M. Meegaskumbura, S. Mohd. Razman, M. D. Morecroft, C. J. Nytch, A. Oliveira, G. G. Parker, S. Pulla, R. Punchi-Manage, H. Romero-Saltos, W. Sang, J. Schurman, S.-H. Su, R. Sukumar, I.-F. Sun, H. S. Suresh, S. Tan, D. Thomas, S. Thomas, J. Thompson, R. Valencia, A. Wolf, S. Yap, W. Ye, Z. Yuan, and J. K. Zimmerman. 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology* 101:1214–1224
- Mills, A. J., S. C. Birch, R. Stanway, O. Huyser, **R. A. Chisholm**, C. Sirami, and D. Spear. 2013. Sequestering carbon and connecting renosterveld through fallowing: a practical conservation approach for the Overberg, Cape Floristic Region, South Africa. *Conservation Letters* 6:255–263
- Condit, R., **R. A. Chisholm**, and S. P. Hubbell. 2012. Thirty years of forest census at Barro Colorado and the importance of immigration in maintaining diversity. *PLOS ONE* 7(11): e49826
- **Chisholm, R. A.** and S. A. Levin. 2012. Linking dispersal and immigration in multi-dimensional environments. *Bulletin of Mathematical Biology* 8:1754–1763
- **Chisholm, R. A.** and B. A. Wintle. 2012. Choosing ecosystem service investments that are robust to uncertainty in multiple parameters. *Ecological Applications* 22:697–704
- **Chisholm, R. A.** 2011. Time-dependent solutions of the spatially implicit neutral model of biodiversity. *Theoretical Population Biology* 80:71–79
- **Chisholm, R. A.** and H. C. Muller-Landau. 2011. A theoretical model linking interspecific variation in density dependence to species abundances. *Theoretical Ecology* 4:241–253
- **Chisholm, R. A.** and S. W. Pacala. 2011. Theory predicts a rapid transition from niche-structured to neutral biodiversity patterns across a speciation-rate gradient. *Theoretical Ecology* 4:195–200
- **Chisholm, R. A.** and S. W. Pacala. 2010. Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proceedings of the National Academy of Sciences* 107:15821–15825
- **Chisholm, R. A.** 2010. Tradeoffs between ecosystem services: water and carbon in a biodiversity hotspot. *Ecological Economics* 69:1973–1987
- **Chisholm, R. A.** and R. J. Taylor. 2010. Body size and extinction risk in Australian mammals: an information-theoretic approach. *Austral Ecology* 35:616–623
- **Chisholm, R. A.** and J. W. Lichstein. 2009. Linking dispersal, immigration and scale in the neutral theory of biodiversity. *Ecology Letters* 12:1385–1393
- **Chisholm, R. A.** 2009. The Ecology, Economics and Management of Alien Invasive Species. In: Levin, S. A. (ed.), *The Princeton Guide to Ecology*. Princeton University Press, 731–739

- Bekessy, S. A., B. A. Wintle, A. Gordon, J. C. Fox, **R. A. Chisholm**, B. Brown, T. Regan, N. Mooney, S. M. Read, and M. A. Burgman. 2009. Modelling human impacts on the Tasmanian Wedge-tailed Eagle (*Aquila audax fleayi*). *Biological Conservation* 142:2438–2448
- **Chisholm, R. A.** and E. Filotas. 2009. Critical slowing down as an indicator of transitions in two-species models. *Journal of Theoretical Biology* 257:142–149
- Bekessy, S., B. Wintle, A. Gordon, **R. A. Chisholm**, L. Venier, and J. Pearce. 2008. Dynamic Landscape Meta-population Models and Sustainable Forest Management. In J. Millsbaugh and F. Thompson (editors), *Models for Planning Wildlife Conservation in Large Landscapes*. Elsevier Science, The Netherlands, 473–500
- **Chisholm, R. A.**, and R. J. Taylor. 2007. Null-hypothesis significance testing and the critical weight range for Australian mammals. *Conservation Biology* 21:1641–1645
- **Chisholm, R. A.** 2007. Sampling species abundance distributions: Resolving the veil-line debate. *Journal of Theoretical Biology* 247:600–607
- **Chisholm, R. A.**, and B. A. Wintle. 2007. Incorporating landscape stochasticity into population viability analysis. *Ecological Applications* 17:317–322
- Taylor, R. J., and **R. A. Chisholm**. 2005. The occurrence of hollows in eucalypts and Ironwood (*Erythrophleum chlorostachys*) in the Gulf region of the Northern Territory and its implications for timber harvesting. *Pacific Conservation Biology* 11:57–63
- Wintle, B. A., S. A. Bekessy, L. A. Venier, J. L. Pearce, and **R. A. Chisholm**. 2005. Utility of dynamic landscape metapopulation models for sustainable forest management. *Conservation Biology* 196:1930–1943
- **Chisholm, R. A.** and M. A. Burgman. 2004. The unified neutral theory of biodiversity and biogeography: comment. *Ecology* 85:3172–3174

#### Other

- **Chisholm, R. A.** 2015. Lessons on diversity from a temperate biome (book review). *Ecology* 96:2314–2315
- O’Dwyer, J. P. and **R. A. Chisholm**. 2013. Neutral Theory and Beyond. In: S. A. Levin (editor), *Encyclopedia of Biodiversity*, 2nd edition, Volume 5. Elsevier, 510–518
- **Chisholm, R. A.** and S. W. Pacala. 2011. Independent species in independent niches behave neutrally: Response. *Oikos* 120:964–965
- **Chisholm, R. A.** 2010. Exponential growth in invasion biology (book review). *Bioscience* 60:314–315

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#### CONFERENCE PRESENTATIONS

- International Conference for Conservation Biology. Kuala Lumpur, Malaysia. July 2019.
- Association for Tropical Biology and Conservation Annual Meeting. Kuching, Malaysia. July 2018.
- Ecological Society of America Annual Meeting. Portland OR, USA. August 2017.
- International Congress for Conservation Biology. Cartagena, Colombia. July 2017.
- Conservation Asia (joint annual regional meeting of the Association for Tropical Biology and Conservation (Asia-Pacific) and the Society for Conservation Biology (Asia)). Singapore. June 2016.
- Association for Tropical Biology and Conservation Asia-Pacific Chapter (plenary). Phnom Penh, Cambodia. April 2015.

- Ecological Society of America Annual Meeting. Sacramento CA, USA. August 2014.
- Association for Tropical Biology and Conservation Annual Meeting. Cairns QLD, Australia. July 2014.
- Society for Industrial and Applied Mathematics Annual Meeting. San Diego CA, USA. July 2013.
- Ecological Society of America Annual Meeting. Portland OR, USA. August 2012.
- Workshop on Critical Transitions in Complex Systems. Imperial College London. London, UK. March 2012.
- Ecological Society of America Annual Meeting. Austin TX, USA. August 2011.
- IUCN International Symposium on Climate Change and Forest Biodiversity Conservation. Beijing, China. July 2011.
- European Conference on Mathematical and Theoretical Biology. Kraków, Poland. July 2011.
- Ecological Society of America Annual Meeting. Pittsburgh PA, USA. August 2010.
- International Congress for Conservation Biology. Edmonton AB, Canada. July 2010.
- World Congress of Environmental and Resource Economists. Montreal QC, Canada. June 2010.
- Fynbos Forum. Oudtshoorn, South Africa. August 2008.
- New England Complex Systems Insitute. Boston MA, USA. October 2007.

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## SERVICE

- Associate editor for *Methods in Ecology and Evolution* 2013 – present
- Handling editor for *Conservation Biology* 2013 – present
- Faculty member of Faculty Opinions (F1000) within the Theoretical Ecology section 2011 – present
- Reviewer for journals including *Nature*, *Science*, *Proceedings of the National Academy of Sciences*, *The American Naturalist*, *Ecology Letters*, *Nature Communications*, *Ecology*, *Proceedings of the Royal Society B*, *Conservation Biology*, *Theoretical Population Biology*, *Ecological Economics*, *EPL (Europhysics Letters)*, *Physics Letters A*, *Journal of Theoretical Biology*, *Theoretical Ecology*
- Reviewer: Springer-Verlag, Sinauer, National Science Foundation
- Membership of professional organisations: Ecological Society of America, Society for Conservation Biology

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## LANGUAGES

- German (professional working proficiency)
  - Spanish (professional working proficiency)
  - Indonesian/Malay (limited working proficiency)
  - Mandarin (elementary proficiency)
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