Article type : MR - Commissioned Material - Meeting Report

Title: Range shifts and local adaptation: integrating data and theory towards a new understanding of species' distributions in the Anthropocene

Authors: Julie Lee-Yaw[1*], Rafael D. Zenni[2], Kathryn A. Hodgins[3], Brendon M. H. Larson[4], Roger Cousens[5], and Bruce L. Webber[6,7]

Author addresses:
1. Department of Botany, University of British Columbia, 6270 University Blvd.,Vancouver, BC, V6T 1Z4, Canada
2. Department of Biology, Federal University of Lavras, Av. Central, S/N Campus Universitário, Lavras, Minas Gerais,37200-000, Brazil
3. School of Biological Sciences, Monash University, Clayton VIC 3800, Australia
4. School of Environment, Resources and Sustainability, University of Waterloo, 200 University Avenue W., Waterloo, ON, N2L 3G1, Canada
5. School of BioSciences, The University of Melbourne, Victoria 3010, Australia
6. CSIRO Land and Water, Centre for Environment and Life Sciences, 147 Underwood Ave, Floreat WA 6014, Australia
7. School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia

* Corresponding Author: lee-yaw@zoology.ubc.ca

ANDINA workshop held at Hotel Tronador in Nahuel Huapí National Park, Argentina, January 2018

The profound changes to Earth's climate, oceans, and land surfaces resulting from human activities have heralded what is referred to as the Anthropocene epoch (Lewis & Maslin, 2015). Species are responding to these changes in complex ways (Lenoir *et al*., 2010; Schweiger *et al*., 2010; Tingley *et al*., 2012), creating one of the most pressing scientific challenges of our time: a need to better understand the effects of environmental change on species' distributions (Pecl *et al*., 2017). Addressing this requirement speaks to our ability to predict and mitigate biodiversity loss as well as declines in ecosystem services. However, rates of introductions, extinctions, and range changes in the Anthropocene have outpaced our ability to fully comprehend these changes to species distributions—let alone provide solutions to any problems these changes create for conservation.

The ANDINA workshops were designed to foster the type of cross-discipline collaboration and debate that advances our understanding of complex challenges to biodiversity. The fourth workshop in the ANDINA series brought together 33 ecologists, social scientists, and evolutionary biologists from five continents to specifically address species' range shifts and the role that local adaptation plays in shaping species' distributions. The workshop was organized around three major themes: the implications of range shifts and local adaptation for conservation; the evolutionary and ecological drivers of range shifts; and the evolutionary and ecological consequences of range expansion and local adaptation. Here, we summarize some of our deliberations on each theme, and outline unresolved issues that require further investigation.

Range shifts and local adaptation from a conservation perspective

Global change and the resulting impacts on species' geographic distributions challenge traditional conservation practices focused on the existing complement of species and resources in a given area (e.g. protected areas and resource holdings; Bonebrake *et al.*, 2018). Specifically, in an era of range shifts and movement (i.e. directly or indirectly arising from anthropogenic environmental change), the community composition of regions is changing, creating novel interactions between species (Schweiger *et al*., 2010) and new challenges for resource users and managers. In light of these changes it is critical for scientists and land managers to both re-evaluate management goals and consider new approaches to conservation.

One consideration for which there was general consensus during the ANDINA workshop, is the need to incorporate different scales of biological organization into management practices. In addition to species and their communities, the distribution of specific alleles and genotypes may be important in the context of changing environments. This need is already incorporated into some adaptive management strategies (e.g. bioengineering and translocation efforts: Dumroese *et al.*, 2015; van Oppen *et al.*, 2015; Prince *et al.*, 2017). However, gaps in our understanding of how diversity at different biological scales is changing, the impact of range shifts on community composition in different areas, and the relative importance of local adaptation to the long-term persistence of species contribute to the increasing uncertainty facing managers.

On a more fundamental level, rapid and widespread changes in species' distributions challenge the very premise of conservation. The question of how individual and societal values drive attitudes towards change, management priorities, and even the science that we do (e.g. Vellend, 2017; Kareiva *et al.*, 2017) was raised at the workshop. For instance, how do we classify (from a conservation perspective) and manage species that have shifted their ranges of their own accord in response climate change and that are having negative impacts on recipient communities (Webber & Scott, 2012)? Do we treat these species the same way as we treat non-native species introduced by humans? As another example, is it time to worry less about individual species and more about maintaining the maximum complement of phylogenetic uniqueness in a region or the adaptive potential of populations (Rodrigues *et al.*, 2005; Tucker *et al.*, 2017)? Meeting delegates had different perspectives on these issues, underscoring the challenges to achieving consensus on how best to apply scientific knowledge to conservation issues. Clearly, a great deal more discussion and development of these topics, involving different stakeholders and experts from other disciplines (e.g. economics, sociology, etc.) is needed.

Ecological and evolutionary drivers of range shifts

Classic niche theory holds that the geographic area occupied by a species (i.e. it's geographic range) represents regions where abiotic conditions are suitable for the survival and reproduction of the species, where the species can contend with the suite of biotic interactions it encounters, and where dispersal (i.e. colonization) has not been prevented (Gaston, 2003; Soberon, 2007). Shifts in species' geographic ranges imply changes to one or more of these ecological factors. For instance, the native ranges of many species have moved upslope or poleward in response to climate change and shifting abiotic conditions (Chen *et al.*, 2011; Sunday *et al.*, 2012; Freeman & Freeman, 2014). Similarly, non-native species invasions occur when dispersal constraints are removed (e.g. species are introduced between continents or moved long distances), often concomitantly releasing species from natural enemies. However, there is tremendous variation in the extent to which species respond to changing circumstances, raising the question: what makes some species more likely to shift their range in response to climate change or to become a successful invader?

Meeting delegates agreed that getting a better handle on the relative importance of different ecological drivers to range limits is necessary to understand variation in native and non-native range changes. Recent syntheses of over-the-edge transplant experiments and niche models have suggested that species are often niche—rather than dispersal—limited (Hargreaves *et al.*, 2014; Lee-Yaw *et al.*, 2016). Yet the majority of the species included in these syntheses were plants and focused on elevational range limits, and most studies experimentally testing the ability of species to contend with conditions beyond the range suffered from one or more methodological issues (Hargreaves *et al.*, 2014). Direct quantification of the demographic effects of different ecological factors influencing range limits is needed in many more taxa and for different types of range limits (i.e. geographical versus elevational limits). Furthermore, the experimental tractability of considering dispersal, abiotic, or biotic drivers of range limits in isolation ignores potential synergies between these factors (Alexander *et al.*, 2015). Empirically quantifying interactions between different range limiting factors remains a huge challenge yet is likely necessary to explain variation in the response of species to novel environments.

The importance of adaptation during range expansion was another unresolved question brought forth during the meeting. Specifically, how often do range changes simply involve tracking suitable yet shifting conditions versus evolution of the niche itself (Wiens *et al.*, 2005)? Likewise, do the introduced ranges of non-native species simply reflect niche filling of previously inaccessible areas, or are they the result of niche shifts following introduction (Atwater *et al.*, 2017)? In both cases understanding the conditions that promote or hinder adaptation during range expansion is important.

Finally, in the conclusion of his 2009 synthesis of range limits, ecologist Kevin Gaston wrote “there may be few truly general patterns as to the determinants of the limits of geographic ranges, with most claimed generalities at least having many exceptions" (Gaston, 2009). Does the extreme variation in climate-mediated range shifts among species (e.g. Angert *et al.*, 2011; Tingley *et al.*, 2012) reflect the idiosyncratic nature of range limits, or, with enough data, will we be able to produce models that allow us to accurately predict the consequences of global environmental change on species' distributions and biodiversity? Perhaps the search for generalities is a question of scale. For instance, even if additional studies continue to support the general conclusion that range limits reflect niche constraints (i.e. Hargreaves *et al*., 2014; Lee-Yaw *et al*., 2016), the specific genes and traits that determine the set of conditions that a species can tolerate along a given niche dimension and the processes that govern the evolution of these traits may differ among species.

Ecological and evolutionary consequences of range expansion and local adaptation

Although ecological and evolutionary processes drive local adaptation and range expansion, the reverse is also true: adaptation and range expansion can impact the very processes that generate change in the first place. For instance, range expansion can place species into novel environments (abiotic and/or biotic) and can lead to new ecological challenges for both the arriving species as well as the recipient community. Range expansion can also result in Allee effects, impacting demographic properties at the expansion front. From an evolutionary perspective, as populations become locally adapted, selection may eliminate genetic variance (Walsh, 2004), limiting the future adaptive potential of populations. Likewise, range expansion can lead to reductions in genetic variation through successive bottlenecks (Hewitt, 1996; Dlugosch *et al*., 2015; Zenni *et al*., 2017) and may lead to the fixing of deleterious alleles through allele surfing (Peichl *et al*., 2013; Travis *et al*., 2007; Hallatsheck & Nelson, 2009). How then do local adaptation and range expansion ultimately impact the dynamics of populations?

Considering local adaptation, a major problem identified during the workshop is that local adaptation is commonly assessed via comparisons of the relative performance of individuals from different populations based on one or more fitness components. Absolute fitness is rarely measured owing to the logistical difficulties of doing so; yet, this information is needed to translate the performance of individuals into the demography of populations (Hargreaves *et al*., 2014). Thus, the impact of "local adaptation" (as most commonly measured) on population dynamics remains unclear. This issue represents a major disparity between theory and empirical work, as many models for range limits assume that range expansion is prevented by the demographic consequences of maladaptation—specifically a resulting lack of dispersers (i.e. range colonizers) from sink populations at the range edge (e.g. Kirkpatrick & Barton, 1997). Without the data necessary to link individual performance to population demography, it is unclear whether peripheral populations truly represent demographic sinks, and the actual impact of local adaptation (or maladaptation) on rates of range expansion.

With respect to consequences of range expansions, workshop delegates concluded that there is often a discrepancy between theoretical models and empirical studies. For instance, a leading evolutionary model for range limits is that low levels of genetic variation limit adaptation at the edge of the range (see discussion in Bridle & Vines, 2006; Sexton *et al.*, 2009). Studies using neutral genetic markers have found mixed support for this hypothesis (Eckert *et al.*, 2008; Excoffier *et al*., 2009). Yet the distribution of relevant variation (i.e. variation that affects phenotype; e.g. Rózsa *et al*., 2016) and consequences for fitness remain unclear in most cases. Tests of other genetic consequences of range expansion (e.g. expansion load; but see González-Martínez *et al*., 2017; Peischl *et al*., 2013; Willi *et al*., 2017) also remain limited, making it unclear whether such effects are common. Likewise, the genetic architecture of adaptation is largely unknown (i.e. number and effect sizes of different variants, their distribution in the genome, and whether they demonstrate dominance; Gilbert & Whitlock, 2017). There was a call amongst workshop participants, especially amongst the theoreticians, for greater empirical treatment of these questions, not only to advance our mechanistic understanding of range dynamics, but to address existing theory and inform the next generation of range limit models.

Finally, consideration of both time and space is likely to be important when thinking about the consequences of range expansion on populations. For instance, are there differences in the types of traits under selection during different stages of range expansion (e.g. dispersal capabilities and mating system during early expansion vs. physiological tolerances after establishment)? If so, then given potential trade-offs between traits (e.g. Jenkins and Hoffmann, 1999), how does the early evolutionary trajectory of populations at the expansion front impact subsequent evolution (Burton *et al*., 2010; Perkins *et al*., 2016), and how might the genetic architecture of adaptation change through time or space as expansion proceeds (Dlugosch *et al*., 2015)? Likewise, how does spatial structure and the configuration of expanding populations influence the genetic consequences of range expansion? These questions remain largely unanswered both theoretically and empirically and represent further steps in understanding the consequences of range expansion for populations.

Conclusions and future challenges

Understanding and addressing the impact of human-mediated environmental change on biodiversity represents one of the greatest challenges of the 21st century. As when tackling any complex issue, there is value in not only pooling collective resources and knowledge, but also in challenging accepted scientific “truths”, debating ideas that do not readily lend themselves to consensus, and raising questions that defy our ability to provide answers using existing technology and methods. The ANDINA series of workshops was created to provide such opportunities for critical debate on research directions and objectives in a safe and egalitarian environment (Cousens, 2017). The fourth ANDINA workshop, with its professional facilitation, small-group breakout sessions, relaxed setting, and myriad opportunities for informal discussion led to lively dialogue on the topic of range shifts and local adaptation in the Anthropocene. These discussions highlighted many gaps in our understanding of the ecological and evolutionary feedbacks that govern species' range shifts. In many cases, the impediments to filling these gaps are large, yet the amalgamation of expert knowledge from diverse participants led to several creative and novel suggestions for empirical and theoretical work to address these gaps—many of which are being implemented in various forthcoming papers from the workshop.

Although the Anthropocene challenges us with complex, global problems, science now operates at scales necessary to tackle these problems. Technology has enabled large, international collaborations, and the generation and sharing of vast amounts of data. Hand-in-hand with increasing ease of communication should be the embracement of diversity in science. The benefits of being a collection of investigators from different parts of the world, from different disciplines, and at different career stages was not lost on the participants of the ANDINA workshop—with many calling for even greater consideration of diversity in future workshops in this series and in science in general. Addressing the planet’s most pressing problems requires “all hands on deck” and collating knowledge across different disciplines, cultures, and peoples is critical to transcending current limits to our understanding of shifting distributions and other changes to biodiversity in the Anthropocene.

Acknowledgements

Funding support for the workshop was provided by the New Phytologist Trust and an award to Roger Cousens by The University of Melbourne. The workshop was chaired by Bruce Webber (CSIRO, Australia), organized by Roger Cousens, Kay Hodgins (Monash University, Australia), Brendon Larson (University of Waterloo, Canada) and Ingolf Kühn (Martin-Luther University, Germany) and involved the following participants: Adam Davis, Amy Angert, Anna Hargreaves, Bruce Maxwell, Cascade Sorte, Dan Atwater, Dave Richardson, Emily Moberg, Erin Cameron, Franck Courchamp, Gretta Pecl, Jake Alexander, Julie Lee-Yaw, Justin Travis, Kate Ostevik, Katrina Dlugosch, Kim Gilbert, Mariana Chiuffo, Marissa Baskett, Mark Kirkpatrick, Martin A. Nunez, Mike Whitlock, Morgan Tingley, Phil Hulme, Rafael D. Zenni, Rob Colautti, Roger Cousens, Spencer Barrett, Swati Patel and Trisha Spanbauer. Michael Williams served as workshop facilitator and was instrumental to the planning and execution of the meeting. His keen ability to keep the meeting on track and to ensure that everyone got a voice during each session was very much appreciated. We thank Mariana Chiuffo and Martin A. Nuñez for local logistics and the Hotel Tronador for their superb hospitality.

References

Alexander JM, Diez JM, Levine JM. 2015. Novel competitors shape species' responses to climate change. *Nature* **525**: 515-518.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, TewksburyJJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecology Letters* **14**: 677–689. doi:10.1111/j.1461-0248.2011.01620.x

Atwater DZ, Ervine C, Barney JN. 2017. Climatic niche shifts are common in introduced plants. *Nature Ecology & Evolution* **2**: 34-43.

Bonebrake TC, Brown CJ, Bell JD, Blanchard JL, Chauvenet A , Champion C, Chen I, Clark TD, Colwell RK, Danielsen F, Dell AI, Donelson JM, Evengård B, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Jarzyna MA, Lee E, Lenoir J, Linnetved H, Martin VY, McCormack PC, McDonald J, McDonald -Madden E, Mitchell N, Mustonen T, Pandolfi JM, Pettorelli N,

Possingham H, Pulsifer P, Reynolds M, Scheffers BR. Sorte CJ, Strugnell JM, Tuanmu M, Twiname S, Vergés A, Villanueva C, Wapstra E, Wernberg T, Pecl GT. 2018. Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews* **93**: 284-305.

Bridle JR, Vines TH. 2006. Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology and Evolution* **22**: 140-147.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**: 1024–1026.

Cousens R .2017. Do we argue enough in Ecology? *BES Bulletin* **48**: 58-61.

Dumroese RK, Williams MI, Stanturf JA, Clair JBS. 2015. Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering. *New Forests* **46**: 947-964.

Dlugosch KM, Anderson SR, Braasch J, Cang FA, Gillette HD. 2015. The devil is in the details: genetic variation introduced populations and its contributions to invasion. *Molecular Ecology* **24**: 2095-2111.

Eckert CG, Samis KE, Lougheed SC. 2008. Genetic variation across species' geographic ranges: the central-marginal hypothesis and beyond. *Molecular Ecology* **17**: 1170-1188.

Excoffier L, Foll M, Petit RJ. 2009. Genetic Consequences of Range Expansions. *Annual Review of Ecology, Evolution, and Systematics* **40**: 481–501.

Freeman BG, Freeman AMC. 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proceedings of the National Academy of Sciences* **111**: 4490–4494.

Gaston KJ. 2003. *The structure and dynamics of geographic ranges*. Oxford, UK: Oxford University Press, Oxford.

Gaston KJ. 2009. Geographic range limits: achieving synthesis. *Proceedings of the National Academy of Sciences* **276**: 1395-1406.

Gilbert KJ, Whitlock MC. 2017. The genetics of adaptation to discrete heterogeneous environments: frequent mutation and large-effect alleles can allow range expansion. *Journal of Evolutionary Biology* **30**: 591-602.

González-Martínez SC, Ridout K, Pannell JR. 2017. Range expansion compromises adaptive evolution in an outcrossing plant. *Current Biology* **27**: 2544-2551.

Hallatsheck O, Nelson DR. 2009. Life at the Front of an Expanding Population. *Evolution* **64**: 193–206.

Hargreaves AL, Samis KE, Eckert CG. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist* **183**: 157–73.

Hewitt GM. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* **58**: 247-276.

Jenkins NL, Hoffmann AA. 1999. Limits to the southern border of *Drosophila serrata*: cold resistance, heritable variation, and trade-offs. *Evolution* **53**: 1823-1834.

Kirkpatrick M, Barton NH. 1997. Evolution of a Species' Range. *The American Naturalist* **150**: 1-23.

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning JC. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* **33**: 295–303.

Lee-Yaw JA, Kharouba HM, Bontrager M, Mahony C, Csergő AM, Noreen AME, Li Q, Schuster R, Angert AL. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters* **19**: 710–722.

Lewis SL, Masin MA. 2015. Defining the anthropocene. *Nature* **519**: 171-180.

van Oppen MJH, Oliver JK, Putnam HM, Gates RD. 2015. Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Scienc*e **112**: 2307-2313.

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis R, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnetved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJB, Strugnell JM, Sunday JM, Tuanmu MN, Vergés A, Villanueva C, Wernberg T, Wapstra E, Williams SE. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**: doi:10.1126/science.aai9214

Peischl S, Dupanloup I, Kirkpatrick M, Excoffier L. 2013. On the accumulation of deleterious mutations during range expansions. *Molecular Ecology* **22**: 5972–5982.

Prince DJ, O'Rourke SM, Thompson TQ, Ali OA, Lyman HS, Saglam IK, Hotaling TJ, Spidle AP, Miller MR. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. *Science Advances* **3**: e1603198

Rodrigues ASL, Brooks TM, Gaston K. 2005. Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? In: Purvis A, Gittleman

JL, Brooks T, eds. *Phylogeny and Conservation*. New York, NY, USA: Cambridge University Press

Rózsa J, Strand TM, Montadert M, Kozma R, Höglund J. 2016. Effects of a range expansion on adaptive and neutral genetic diversity in dispersal limited Hazel grouse (*Bonasa bonasia*) in the French Alps. *Conservation Genetics* **17**: 401-412.

Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kühn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T, Potts SG, Pyšek P, Stout JC, Sykes MT, Tscheulin T, Vilà M, Walther G-R, Westphal C, Winter M, Zobel M, Settele J. 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews* **85**: 777–795.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. *Annual Reviews in Ecology and Evolution* **40**: 415-436.

Soberón J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**: 1115-1123.

Sunday JM, Bates AE, Dulvy NK. 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* **2**: 686–690.

Tingley MW, Koo MS, Moritz C, Rush AC, Beissinger SR. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* **18**: 3279–3290.

Travis JMJ, Münkemüller T, Burton OJ, Best B, Dytham C, Johst K. 2007. Deleterious mutations can surf to high densities on the wave front of an expanding population. *Molecular Biology and Evolution* **24**: 2334–2343.

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* **92**: 698–715

Walsh B. 2004. Population- and quantitative-genetic models of selection limits. In: Janick J, ed., *Plant Breeding Reviews.* doi:10.1002/9780470650240.ch9.

Webber BL, Scott JK. 2012. Rapid global change: implications for defining natives and non-natives. *Global Ecology and Biogeography* **21**: 305-311.

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **36**: 519-539.

Willi Y, Fracassetti M, Zoller S, Van Buskirk J. 2018. Accumulation of mutational load at the edges of a species range. *Molecular Biology and Evolution* doi: 10.1093/molbev/msy003.

Zenni RD, Dickie IA, Wingfield MJ, Hirsch H, Crous CJ, Meyerson LA, Burgess TI, Zimmermann TI, Klock MM, Siemann E, Erfmeier A, Aragon R, Montti L, Le Roux JJ. 2017. Evolutionary dynamics of tree invasions: complementing the unified framework for biological invasions. *AoB Plants* **9**: plw085.