

IN FOCUS

Heating up relations between cold fish: competition modifies responses to climate change



Example of an Arctic charr, in spawning colouration, collected by gill nets in a Norwegian lake whilst studying differences in physiological response to ice-cover. Image by Anders Finstad.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal, O. (2011) Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology*, **80**, 539–547.

Most predictions about species responses to climate change ignore species interactions. Helland and colleagues (2011) test whether this assumption is valid by evaluating whether ice cover affects competition between brown trout [*Salmo trutta* (L.)] and Arctic charr [*Salvelinus alpinus* (L.)]. They show that increasing ice cover correlates with lower trout biomass when Arctic charr co-occur, but not in charr's absence. In experiments, charr grew better in the cold, dark environments that typify ice-covered lakes. Decreasing ice cover with warmer winters could mean more trout and fewer charr. More generally, their results provide an excellent example, suggesting that species interactions can strongly modify responses to climate change.

The forecast for rapid climate change calls for ecologists to predict how climate change will alter the fate of species across the globe. In response, ecologists have produced a vast ensemble of models that predict how species might react to future climates based on their distributions or physiologies (Buckley *et al.* 2010). These models almost invariably omit biotic interactions (Gilman *et al.* 2010) and therefore assume that species' responses to climate change can be evaluated in a community ecology vacuum (McCarthy 2011). Undoubtedly this approach offers a first approximation and might be necessary without more detailed information. However, species' niches are not separable like oil and water into disparate abiotic and biotic components – these components interact to produce the niche (Hutchinson 1957). Thus, changes in abiotic conditions (e.g., climate change) can affect fitness both directly and indirectly by modifying species interactions (Dunson & Travis 1991; Visser &

Holleman 2001; Winder & Schindler 2004; Gilman *et al.* 2010). Textbook examples include differential competition among *Tribolium* flour beetles depending on temperature and humidity (Park 1954), and differential competition among *Drosophila* flies depending on temperature (Davis *et al.* 1998). More recently, Tylianakis *et al.* (2008) report that climate change affects every interaction type. However, sometimes the direct effects of climate might overwhelm the indirect influence of species interactions (Mutshinda, O'Hara & Woiwod 2011). So how do we know when to consider species interactions and when we can safely ignore them? Helland and colleagues (2011) provide an example of the research that will be needed to answer this question.

As winter arrives, most ecologists in temperate climes settle into their cosy offices to write *In Focus* articles and analyse data collected in fairer weather. Yet, winter might be the most interesting season to study northern lake fish communities because survival during this season determines population persistence. Helland *et al.* (2011) combined careful measurements of fish physiology with observations of brown

*Correspondence author. E-mail: mark.urban@uconn.edu

trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) abundances across both time and space. They unite these data in a common correlative and mechanistic framework to argue convincingly that interspecific competition mediates how warmer winters affect trout abundances. Seldom do studies integrate across venue, space and time so elegantly to paint a picture of community interactions as a function of climatic variation.

Winter for a Norwegian lake fish is cold and dark. Ice covers the lake surface and snowfall darkens the waters. Most fish hunker down and try to minimize losses of mass. However, winters are warming, and the ice cover on lakes has diminished. In the Northern Hemisphere, ice covers water bodies 12 days less than it did 100 years ago (Magnuson *et al.* 2000), presumably because global temperatures have risen 1.2 °C over the past century. Future climate projections include a possible tripling of this warming rate in the next century (IPCC 2007), which will likely accelerate decreases in lake ice. This decrease in ice cover conveys bad news for the Arctic charr, but good news for its competitor, the brown trout.

Across 144 Norwegian lakes, duration of ice cover does not alter trout biomass – and this is key – as long as their competitor, the Arctic charr, is absent. When Arctic charr co-occur with brown trout, trout biomass decreases with every day of extra ice cover. Across a 25-year data set of trout and charr abundances in a single lake, longer ice durations and higher Arctic charr abundances resulted in less trout biomass. Helland *et al.* (2011) then explore the purported mechanism of temperature- and light-dependent differences in foraging and growth between the two species. Laboratory and outdoor experiments indicate that Arctic charr grow more and consume more calories than brown trout at winter temperatures and in darkness (Helland *et al.* 2011). These results suggest that charr can extract more resources in the winter and thus out-compete trout during this season.

Critically, this study highlights the complexity of climate's influence on species interactions. Brown trout (*Salmo trutta*) out-compete Arctic charr (*Salvelinus alpinus*) under summer skies. However, winter ice cover reverses this situation. Arctic charr are the world's most northerly distributed freshwater fish, and they perform well under winter conditions. Hence, the relative success of the two species switches seasonally, and this seasonal switch presumably facilitates their coexistence. A change in climate that shortens winter could make coexistence less likely and brown trout more plentiful. Arctic charr should persist in large lakes with sufficient habitat diversity where they can avoid direct summer competition, but could decrease in small lakes with intense summer competition. Thus, understanding climate responses requires understanding species interactions integrated across all seasons (Yang & Rudolf 2009).

Despite the emphasis on heat stress for determining species' fitness and distributions, warmer winters might often determine species' responses to climate change by lessening cold stress (Crozier 2003). Climate change will amplify any fitness effects sensitive to winter temperature. MacArthur

(1972) suggested nearly 40 years ago that species interactions will set equatorward range limits and abiotic tolerances will set poleward limits. Thus, it seems reasonable that warmer winter conditions would enhance brown trout success. But this study suggests a more nuanced perspective. Shifting ranges in response to climate change also might involve changing species interactions at poleward limits because biotic interactions and abiotic constraints are often inextricably linked.

We can expect similar changes to lake community interactions world-wide. Ice cover has declined on most lakes for which long-term data exist (Magnuson *et al.* 2000). These changes to ice cover can affect species interactions and abundances beyond trout and charr, including other fish species, zooplankton and phytoplankton (Blenchner, Omstedt & Rummukainen 2002; Magnuson 2010). Importantly, decreasing ice cover on lakes can reduce anoxia and the probability of winter fish kills (Fang & Stefan 2009). Ice-influenced winter kills often determine fish distribution among shallow temperate lakes, and fish occurrence in turn alters lake community and ecosystem properties (Carpenter *et al.* 1987; McPeck 1990; Wellborn, Skelly & Werner 1996). With climate change, we can expect more of the types of species that can coexist with fish and fewer species that only survive in fishless lakes.

And yet not all species' responses to climate change will depend on species interactions. For instance, Mutshinda *et al.* (2011) found that interactions among 12 moth species only weakly explained multispecies' population dynamics when compared to direct contributions from weather variation and intraspecific interactions. This finding provides some hope that ecologists can ignore some of the complexities inherent with incorporating species interactions (McCarthy 2011). Adding species interactions to climate change predictions is difficult for we often know little about species interaction strengths and their climate dependencies, and we urgently need to make climate change predictions across many taxa and biomes in a short time. Clearly, the effect of species interactions on climate change responses will differ among communities. The trick is to focus on those species interactions that are most likely to alter predictions substantially. The work by Helland *et al.* (2011) provides a good example – two top predators foraging on overlapping prey in the same place provide a recipe for strong competition.

So why does climate change matter for fish and not moths? The answer likely involves differences in approach, taxa and ecosystems. The Mutshinda *et al.* (2011) study relies on a correlative partitioning of variance among species which were not chosen in advance based on their interaction strengths. Many ecologists have argued that herbivorous insects often do not compete strongly because different species use different host plants, and many insect populations undergo large-amplitude fluctuations in abundance, even in constant climates (Lawton & Strong 1981). In contrast, Helland *et al.* (2011) begin with a strong species interaction supported by correlative patterns to which they add experiments that evaluate mechanism. Water bodies also integrate temperature

differently than terrestrial environments and are less likely to be buffeted by fine-scale variation in climatic drivers.

Ecologists will not usually have the resources to perform such in-depth mechanistic investigations; a correlative approach often will be all that is feasible. However, we suggest that it is possible to perform mechanistic studies for the species that interact most strongly in a community – the so-called community module approach to community ecology (Holt 1997; Gilman *et al.* 2010). This recommendation focuses attention on identifying which species interact strongly and which interactions depend on climate. Thus for a given system, one should assess the likely influence of different types of interactions and use this information to guide the inclusion of species interactions into predictions. Identifying such interactions requires the specific knowledge that comes from the underrated pursuit of natural history in conjunction with mechanistic modelling and experimental ecology, all harnessed for the aims of climate science. A particularly valuable approach is to combine intense local studies with broader correlative approaches. The study by Helland *et al.* (2011) is in this respect exemplary, and we encourage future studies that do the same. Every link in a community of interacting species provides a potential opening for climate change impacts, and strong linkages can both amplify and buffer community responses. Grasping the nettle of species interactions is essential for developing firm predictions about future species distributions, extinction risks and ecosystem processes in our rapidly warming world.

Acknowledgements

This paper is a product of a working group entitled 'Mechanistic distribution models: Energetics, fitness, and population dynamics' jointly sponsored by NESCent and NCEAS, and organized by J.T., R.D.H., L. Buckley and M. Angilletta.

MARK C. URBAN^{1,*}, ROBERT D. HOLT², SARAH E. GILMAN³ and JOSHUA TEWKSBURY⁴

¹*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA;* ²*Department of Biology, University of Florida, Gainesville, FL, USA;* ³*Joint Science Department, The Claremont Colleges, Claremont, CA, USA;* and ⁴*Department of Biology, University of Washington, Seattle, WA, USA*

References

- Blenchner, T., Omstedt, A. & Rummukainen, M. (2002) A Swedish case study of contemporary and possible future consequences of climate change on lake function. *Aquatic Sciences*, **64**, 171–184.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L., Rissler, L.J. & Sears, M.W. (2010) Contrasting correlative and mechanistic models of species ranges: putting concepts into practice. *Ecology Letters*, **13**, 1041–1054.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D. & He, X. (1987) Regulation of lake primary productivity by food web structure. *Ecology*, **68**, 1863–1876.
- Crozier, L. (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, **135**, 648–656.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Dunson, W.A. & Travis, J. (1991) The role of abiotic factors in community organization. *American Naturalist*, **138**, 1067–1091.
- Fang, X. & Stefan, H.G. (2009) Simulations of climate effects on water temperature, dissolved oxygen, and ice and snow covers in lakes of the contiguous United States under past and future climate scenarios. *Limnology and Oceanography*, **54**, 2359–2370.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.
- Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal, O. (2011) Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology*, **80**, 539–547.
- Holt, R.D. (1997) Community modules. *Multitrophic Interactions in Terrestrial Systems, 36th Symposium of the British Ecological Society* (eds A.C. Gange & V.K. Brown), pp. 333–349, Blackwell Science, Cambridge, Mass.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 145–159.
- IPCC (2007) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.
- Lawton, J.H. & Strong, J.D.R. (1981) Community patterns and competition in folivorous insects. *American Naturalist*, **118**, 317–338.
- MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper and Row, New York.
- Magnuson, J.J. (2010) History and heroes: the thermal niche of fishes and long-term lake ice dynamics. *Journal of Fish Biology*, **77**, 1731–1744.
- Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., Card, V., Kuusisto, E., Granin, N.G., Prowse, T.D., Stewart, K.M. & Vuglinski, V.S. (2000) Historical Trends in Lake and River Ice Cover in the Northern Hemisphere. *Science*, **289**, 1743–1746.
- McCarthy, M.A. (2011) Breathing some air into the single-species vacuum: multi-species responses to environmental change. *Journal of Animal Ecology*, **80**, 1–3.
- McPeck, M.A. (1990) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology*, **71**, 83–98.
- Mutshinda, C.M., O'Hara, R.B. & Woiwod, I.P. (2011) A multispecies perspective on ecological impacts of climate forcing. *Journal of Animal Ecology*, **80**, 101–107.
- Park, T. (1954) Experimental studies of interspecies competition. 2. Temperature, humidity and competition in two species of *Tribolium*. *Physiological Zoology*, **27**, 177–238.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecological Letters*, **11**, 1351–1363.
- Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B. Biological Sciences*, **268**, 289–294.
- Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.
- Winder, M. & Schindler, D.E. (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, **85**, 2100–2106.
- Yang, L.H. & Rudolf, V.H.W. (2009) Phenology, ontogeny, and the effects of climate change on the timing of species interactions. *Ecology Letters*, **13**, 1–10.

Received 1 February 2011; accepted 28 February 2011
Handling Editor: Corey Bradshaw