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Special Section Introduction: Socioecological Disequilibrium in the Circumpolar North

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Abstract

Despite the evident challenges posed by arctic environments past and present, and despite the widespread acknowledgement that human population histories in the Arctic have historically been quite dynamic, it is often assumed that traditional pre-colonial populations were in perfect equilibrium with their environment, that they were perfectly adapted to their local environmental conditions. This adaptationist assumption is strongly challenged by recent research in ecology that has shown that many high-latitude ecological communities are in fact far from equilibrium with environmental conditions. Here we briefly introduce the notion of disequilibrium and the papers making up this special section. Ranging from the European Palearctic to the predicaments faced by contemporary populations in the circumpolar North, this collection presents a solid comparative evidence base for this new perspective. Together, these papers underline that adaptation – defined classically as the outcome of selection matching a particular feature or behaviour to the social or natural environment – cannot be assumed but needs to be empirically demonstrated. The papers also offer numerous qualitative and quantitative avenues for how to conduct such empirical investigations.

Keywords Arctic · Circumpolar north · Disequilibrium · Historical ecology · Local and traditional ecological knowledge · Indigenous knowledge

Introduction

Adaptation is defined as the match of particular features – anatomical, behavioural, cultural – to a given social or natural environment (Table 1; Laland and Brown 2002). For non-human species at least, the environment is seen as one if not the key benchmark against which adaptation can be measured. Equilibrium is a key notion in ecological research, where systemic change over time is often thought to proceed in cycles where ecosystems oscillate between different, more or less stable states or equilibria (Holling 1973). When a given organism is able to track changes in climate or environment it is seen to be in equilibrium. Notably, such cyclical resilience models are now also widely applied to human socio-ecological constellations, where the notion of the 'environment' is broadened to include social and political components (e.g., Redman 2005; Walker *et al.* 2006; Nelson 2011; Bradtmöller *et al.* 2017). While ecological disequilibrium is not an entirely new concept, recent research in biogeography, especially in the Arctic, suggests that ecological equilibria may, in fact, be rare when the spatial and temporal dimensions – past climate dynamics or anticipated future climate change – are fully accounted for (Normand *et al.* 2013; Svenning and Sandel 2013; Svenning *et al.* 2015). Specifically with regard to flora, Svenning and Sandel (2013: 2) define 'vegetation to be in equilibrium with climate when no climate-driven directional changes would occur in species composition and richness, vegetation structure (e.g., biomass, individual size structure) or other aspects of vegetation-controlled ecosystem structure (e.g., amount of coarse woody debris) in the absence

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Table 1 The evolutionary classification of a given trait as adaptation and its alternatives. The classified traits can be biological or cultural

Evolutionary trait classification	Description
Punctuated equilibrium	Rapid change in populations and communities
Adaptive behaviour/ adaptability	Adaptive behaviour is functional behaviour that increments reproductive fitness
Adaptation	An adaptation is a character favoured by natural selection for its effectiveness in a particular role
Current adaptation	A current adaptation is an adaptation that has remained adaptive because of continuity in the selective environment
Past adaptation	A past adaptation is an adaptation that is no longer adaptive because of a change in the selective environment
Exaptation	An exaptation is a character that now enhances fitness but was not built by natural selection for its current role
Dysfunctional by-product	A dysfunctional by-product is a character that neither enhances fitness nor was built by natural selection

of further climate change'. In contrast, disequilibrium states may, they suggest, significantly reduce ecosystem function and may ultimately lead to deleterious maladaptations.

A conference in 2015 at the Arctic Research Center, Aarhus University, addressed the question of whether similar kinds of disequilibrium conditions could also be discerned in human populations and their cultural constellations in the circumpolar North. The collection of papers presented in this special section of *Human Ecology* represents a selection of those presented at that conference. They effectively showcase the diversity of observations, empirical data, and analytical approaches taken by leading arctic researches with regard to this question. This introduction first expands on the definition of socio-ecological disequilibrium and the processes underlying it, and then briefly discusses the following papers. We articulate the notion of disequilibrium as defined in ecology with concepts such as landscape learning (Rockman 2009a) and Local and Traditional Ecological Knowledge/Indigenous Knowledge (LTEK/IK; see Berkes *et al.* 2000) used in archaeology and anthropology. We conclude that, counter to the oft-held assumption of a hand-in-glove fit between traditional societies' social and technological strategies and their environments, disequilibrium may be widespread or even ubiquitous, especially and unsurprisingly under situations of either migration or rapid climate change. When using the label 'traditional societies' we here include all non-industrial communities – prehistoric, historic, and contemporary – but are as such agnostic about their degree of contact with or acculturation into neighbouring societies and their economies. We also use the label 'human sciences' as shorthand for all those disciplines concerned with *Homo sapiens* in a biocultural perspective. This includes but is not limited to archaeology, physical and social anthropology, human behavioural and political ecology, as well as the study of literature and the arts. While the number of societies covered in this special section is small, the disequilibrium perspective raises important points about how we view past arctic populations and the adaptive fit to their environment. Although the temporal and, at times, the geographic scales of the research presented here are large, this perspective may have implications for how we see contemporary populations adapting to the anthropgeneic climate changes so radically amplified in high latitudes.

Ecological Disequilibrium and the Human Sciences

The concept of ecological disequilibrium was introduced to account for the time lags often found in the dynamics of species distributions (Delcourt and Delcourt 1983). Ecological disequilibrium could explain why a species could be found in an area where the environment had become unsuitable for the species' long-term persistence, but the populations were not yet driven to extinction. In another situation, a species could be absent from an area with suitable environmental conditions because it had not yet had sufficient time to disperse to the area (Svenning and Sandel 2013). There is mounting evidence that ecological disequilibrium is widespread and affects the diversity of ecological communities worldwide (Svenning *et al.* 2015). The appreciation of particularly rapid contemporary climate change in the Arctic and the role of glacial dynamics makes the notion of ecological disequilibrium particularly relevant for arctic ecosystems (Normand *et al.* 2013). Species distributions are often described by leading and trailing edges relative to environmental constraints such as temperature. In a warming climate, the leading edge would be at the highest latitude and altitude and the trailing edge would be at the lowest latitude and altitude. Leading-edge disequilibrium can be caused by organisms migrating into a novel environment, by intrinsic demographic dynamics that keep a given population below or above carrying capacity, or through changing community composition. Trailing-edge disequilibria can be underwritten by long generation time that effectively prevent adaptation to changing environments through selection, or by delayed responses of ecological communities or ecosystems to changing conditions. A shared feature of both types of disequilibrium is their evolutionary outcome over time, ultimately leading to adaptive lags and maladaptations. In the slow-to-recover high-latitude environments, humans are another important agent that can create ecological legacies – landscape disturbances and changes in vegetation structure and composition – of considerable spatial and temporal extent (cf. Normand *et al.* 2017). Recently, it has also been shown that such vegetation changes or lack thereof are likely to drive variation in the birds and mammals, (e.g., reindeer) that feed on tundra vegetation (Wheeler *et al.* 2018).

Laland and Brown (2006) discuss such adaptive lags and disequilibria with specific reference to humans' ability to also modify their environments via ecosystem engineering or niche construction. Building on the idea of evolutionary neutral or even deleterious traits as a regular feature of many organisms (Eldredge and Gould 1972), and contrary to adaptationist assumptions, they argue that adaptive mismatches or disequilibria are a common occurrence. They further argue that the extensive and pervasive ways in which humans modify, build, and carry with them important niche components (clothing, tents, crops, domesticated animals) allow them, on the one hand, to tolerate high degrees of ecological disequilibrium and, on the other, to counteract disequilibria caused by changes in external environments to a significant degree, whilst at the same time acting as potentially major disturbance for many other organisms (Odling-Smee *et al.* 2003; Shennan 2006; Laland and O'Brien 2010; Riede 2012). However, humans, too, have limits to their adaptability. Technology is classically defined as "the extra-somatic means of adaptation for the human organism" (Binford 1962: 218). The knowledge underlying the creation and appropriate use of these technologies, and of natural resources and ecosystem services is often summarily referred to as Local and Traditional Ecological Knowledge or Indigenous Knowledge (LTEK/IK). This notion can in turn be usefully linked to the idea of landscape learning, essentially adding a diachronic dimension and thereby stressing that LTEK/IK also needs to be acquired and refined over time. Numerous archaeological and historical case studies have shown how humans moving into new environments, in particular, are prone to disequilibrium – maladaptation grounded in a lack of knowledge about local ecological conditions or appropriate technologies – and hence also to significant population collapses or declines (Kelly 2003; Riede 2007, 2014; Rockman 2009b). Likewise, such disequilibria can also be detected in the recent past, for instance among arctic reindeer hunters (Minc and Smith 1989; Stenton 1991) as well as in the present, where both rapid climate change and colonial and post-colonial impacts have threatened the lives and livelihoods of arctic communities (Crate 2006, 2008; Willerslev 2009).

Focusing on knowledge and learning as the foundation of socio-ecological disequilibrium also highlights the potential for adaptation. Human populations have persisted in the Arctic over many millennia, revealing the evident ability to learn landscape knowledge and to translate this knowledge into action. But people's ability to forsee the future may in fact be limited (Mesoudi 2008), and this is important in several ways: a lack of ecological knowledge can occur when people move into novel landscapes, it can occur when climates and environments change rapidly, or when human interventions in the environment lead to unpredicted and unintended changes. The case studies collected together in the special section add to that roster.

From the Palearctic to the Present – Case Studies in Arctic Disequilibrium

This special section consists of five papers that range chronologically from the Late Pleistocene to the present, and geographically virtually the entire circumpolar North from Europe (Riede and Pedersen 2018), to Siberia (Krupnik 2018), to Alaska (Krasinski 2018), and the Canadian Arctic and Greenland (Prentiss *et al.* 2017; Jackson *et al.* 2018; Tejsner and Veldhuis 2018). The papers are arranged chronologically and underline that arctic communities have indeed been and continue to be vulnerable in relation to rapid climatic and environmental changes, but also that they can show remarkable flexibility and adaptability congruent with many circumpolar ontologies that facilitate flexible kinship structures and an inherently resilient way of life and approach to objects, people, and the environment (e.g., Brody 2001). This challenges us to rethink how we may better consider the interaction of mostly Western conceptions of exposure and indigenous cultural versatility among circumpolar populations. Importantly, this combination of adaptability and vulnerability holds true for populations pursuing very different kinds of economic strategies.

Methodologically, the papers range from quantitative to qualitative. Particularly noteworthy here is the application of phylogenetic analyses by Prentiss and colleagues to cultural datasets (see also Prentiss *et al.* 2014, 2015). Based on the conceptualisation of cultures as communities of knowledge and practice, this method articulates both with the idea of LTEK/IK and evolutionary biology, where phylogenetic approaches often constitute the methodological backbone for testing whether particular traits are adaptations or simply by-products of evolutionary processes (Harvey and Pagel 1991; Pagel 1999). Such cultural phylogenetic methods are seeing increasingly widespread application in the human sciences (including the social sciences and humanities; Mace and Pagel 1994, 1997; Collard *et al.* 2006; Collard and Shennan 2008,). Elsewhere, our own and others' research discusses in detail how different kinds of archaeological and ethnographic data and these methods could be applied to a range of case studies in specifically the Palearctic, Arctic and Subarctic (see Jordan and O'Neill 2010; Riede 2010, 2011; Jordan 2015).

Riede and Pedersen likewise take a quantitative approach, although they focus primarily on ways to reconstruct population dynamics using a variety of ecological and artefactual proxies. In turn, these proxies facilitate a discussion of the degree to which initial adaptations to Late Pleistocene Palearctic environments stood the test of time and of changing environs for these pioneering populations. They stress that understanding demography is key to understanding evolution (Metcalf and Pavard 2007), a sentiment that also holds true for past human demography and cultural evolution (Shennan 2008). Potentially, this case study has implications not only for how we understand past cultural change in the Palearctic, but also how we think about the relationship between demography, adaptation and long-term viability of contemporary arctic populations.

Although such quantitative approaches may offer the most seamless integration with disequilibrium theory as defined in ecology, the detailed qualitative accounts offered by Krasinski, Jackson and colleagues, and Krupnik contribute no less powerfully to the debate and draw on many years' work by many scholars. Krasinski demonstrates how people in the Susitna Valley in southcentral Alaska dealt with long-term changes in the environment by modulating their settlement patterns and economic strategies. The data resolution in this deep-time case study may not be sufficient to detect to what degree these shifts involved temporary disequilibria, but the case study demonstrates how human communities persist in the face of such changes by accumulating landscape knowledge and by transforming natural environments into cultural landscapes.

Jackson *et al.*'s case study contrasts with this example by showing how a Norse agro-pastoral community attempted to cope after migrating into a new environment in Greenland. Although superficially similar to their ancestral homelands in Iceland and Norway, Greenlandic ecology differed in subtle but important ways: less navigable seaways, ground that was frozen longer. For the Greenland Norse, this dual challenge was further compounded by the impact of the so-called Little Ice Age, the onset of which is dated to shortly after their arrival in Greenland. It is evident from Jackson and colleagues' case study that these Viking descendants ultimately suffered from both leading- and trailing-edge disequilibrium, which led to the eventual disappearance from Greenland sometime in the middle of the fifteenth century. In this way, the case study mirrors the findings of Riede and Pedersen in that migration, climate change, and cultural inertia – together with an additional lack of economic/ecological connectivity – combine into adaptive constraints that prevent communities from responding adequately and adaptively.

Igor Krupnik's contribution summarises key results from the Smithsonian Institution's *Arctic Crashes* project. It is well known that many arctic organisms, especially many large mammals such as reindeer, experience substantial and difficult to predict population declines (but see Hansen *et al.* 2013; Bårdsen *et al.* 2017). These may be amplified in recent times due to anthropogenic climate change and other human interventions in the circumpolar North and Krupnik discusses how contemporary communities attempt to deal with these fluctuations. For many communities, the outlook may be bleak, but the kind of transdisciplinary research exemplified by Krupnik's contribution also offers prospective strategies for coping with the great challenge of rapidly changing climate and environment in our time. Finally, the contribution of Veldhuis and Tejsner similarly demonstrates how human populations in the Arctic, specifically in Greenland, respond bioculturally to such climatic and environmental changes. The resolution afforded by the combination of qualitative ethnographic and quantitative demographic datasets utilised here underlines that people are not passive in the face climate change, but also that human communities are by no means able to fully buffer the negative effects of such external environmental forcing.

Future Perspectives

The papers in this Special Section of *Human Ecology* together chart the successes and failures of arctic societies from the deep time of the Late Pleistocene to the present. They show how creatively and persistently human communities have found social, technological, and economic/ecological solutions to the challenges of living at high latitudes. Inspired by the notion of socio-ecological disequilibrium, these papers also stress, however, that perfect adaptations do not simply emerge and that they may in fact be rare. Instead, constant changes in biotic and abiotic environmental factors as well as, in the case of human societies, social parameters lead to greater or lesser degrees of disequilibrium. The colonization of new lands is one scenario, here considered by Krasinski, Riede and Pedersen, Jackson *et al.* and Prentiss *et al.*, in which disequilibrium emerges. This friction between selective pressures and the behaviour, demographic viability and/or distribution of a given group is the background and precondition for subsequent adaptations (as documented here by Krasinski, and Prentiss *et al.*), but also the background for potential societal collapse (as suggested by Jackson *et al.* and Riede and Pedersen). The archaeological record of the North shows that the finely-tuned social and technological systems of arctic adaptations have taken a long time to evolve (Hoffecker 2005). These papers demonstrate precisely this time-depth to how human groups find their place within wider arctic ecological communities. In doing so, they add further substantial evidence for how inter- and transdisciplinary historical ecological research can contribute to not only better understanding past socio-ecological changes but also to reflections on how such changes can be met and mananged in the present and future (see also Barthel *et al.* 2013a, b; Armstrong *et al.* 2017).

The spatial and temporal resolution of the data presented in the archaeological case studies are generally low when compared to those from more recent periods or the ethnographic present. Owing to their temporal depth, they do, however, offer the opportunity to link observed behaviours to demographic and cultural evolutionary consequences. And this has major implications for how we view those case studies concerned with living communities (Krupnik, and Veldhuis and Tejsner in this volume). Those communities, too, show evidence of significant behavioural variability and of rapidly changing environmental and social parameters that struggle to find the hand-in-glove fit we might label adaptation. The notion of socioecological disequilibrium underscores the fragility of life at high latitudes, especially during periods of pronounced climatic, environmental, and societal change. The well-being and survival of present arctic communities rely on finding viable long-term solutions to these challenges. Perhaps the legacies of past adaptations can provide inspiration and resources. Interestingly, and importantly, arctic communities have so far been resilient to pronounced climatic, environmental, and societal change, despite persistent socioecological disequilibrium. This heritage of robustness may be important as arctic communities face future environmental perturbations. We hope that this collection of papers contributes to better understanding past human socio-ecological adaptations – and their limits – in the Arctic and potential adaptations for the present and future. How we conceptualise and measure successful arctic adaptations, and whether disequilibrium rather than adaptation is the rule in high latitudes, has potentially significant implications for how we interpret and understand arctic adaptations and livelihoods in the future.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Informed Consent Not applicable.

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