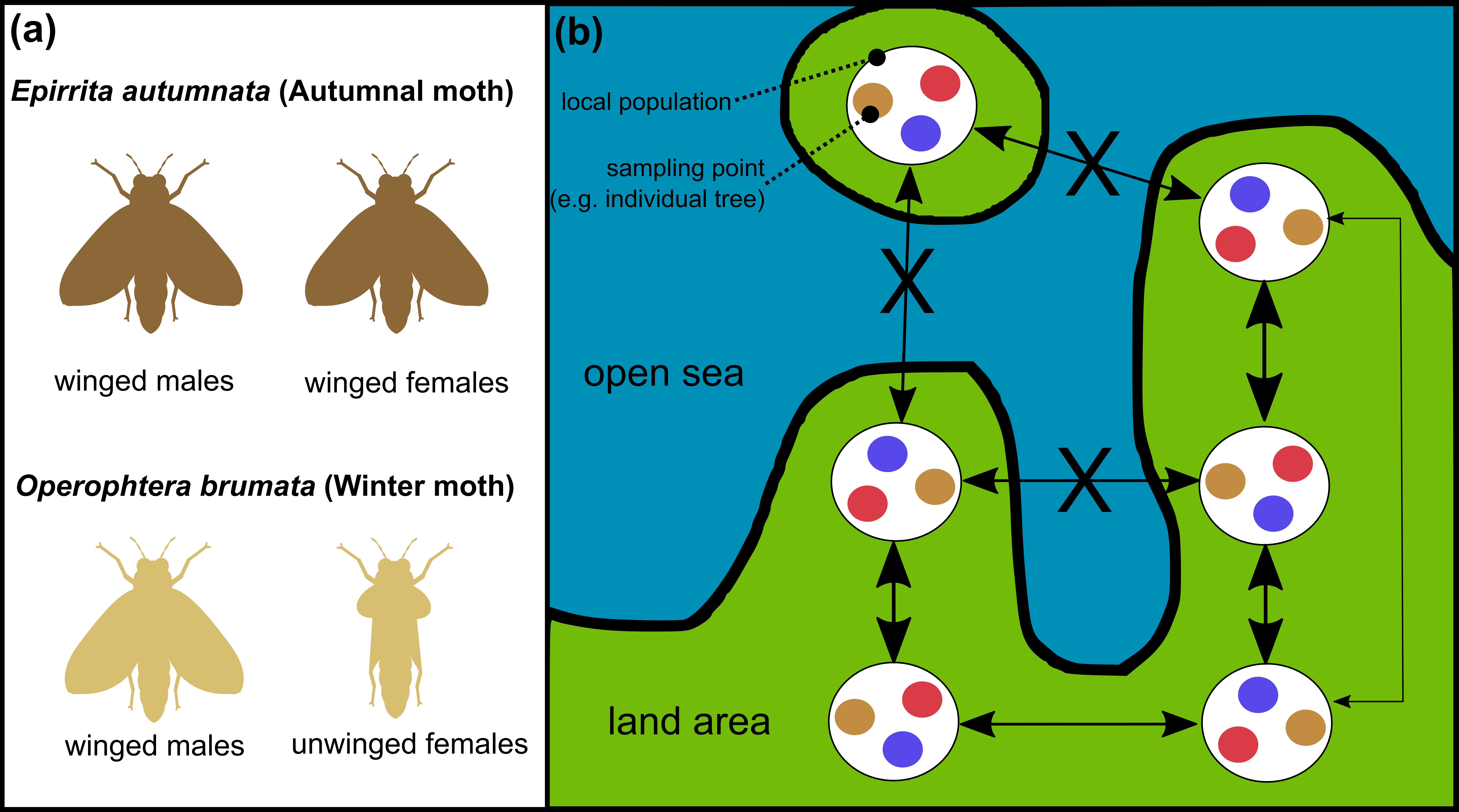
**Spatial synchrony of population dynamics: empirical testing of mechanisms**

In Focus: Vindstad, O.P.L., Jepsen, J.U., Yoccoz, N.G., Bjørnstad, O.N., Mesquita, M.d.S. & Ims, R.A. (2019) Spatial synchrony in sub‐arctic geometrid moth outbreaks reflects dispersal in larval and adult life cycle stages. *Journal of Animal Ecology*

Spatial synchrony of population dynamics is a common phenomenon, but the understanding of underlying mechanisms is supported more by theoretical than empirical studies. Vindstad *et al.* (2019) use a 19-year dataset on two moth species to disentangle the effects of different drivers of dispersal on synchrony of populations. They show that geographic distance, species dispersal capabilities, a dispersal barrier, and the prevailing wind direction are all factors that influence spatial synchrony. With current climate change and ongoing habitat fragmentation, understanding how dispersal influences spatial synchrony of population fluctuations, and the effect on population viability, is essential to predict future impacts on our ecosystems.

Spatial autocorrelation, where closer samples are more similar, is often considered a nuisance for many field ecologists as independent samples are an assumption of many statistical tests (Robertson 1987; Legendre 1993; Legendre *et al.* 2004). However, variation in population dynamics across space and time (spatiotemporal variation) inherently involves spatial autocorrelation, meaning that this is something that we need to understand in order to achieve a predictive understanding of the causes of population fluctuations (Liebhold, Koenig & Bjørnstad 2004; Fortin & Dale 2009). Spatial synchrony is a special type of spatial autocorrelation that refers to spatial covariation in population density fluctuations, i.e. variation through time (Liebhold, Koenig & Bjørnstad 2004). Measuring synchrony is primarily done by correlating changes in population growth rates over time between two populations (Bjørnstad, Ims & Lambin 1999; Buonaccorsi *et al.* 2001). A high correlation suggests they are synchronous, with similar patterns in the increase and decrease of populations, while a low correlation suggests that temporal fluctuations are not similar between the populations. A general pattern that is observed is that synchrony in population dynamics declines with increasing geographic distances between populations, and different species experience different strengths of this effect (Hanski & Woiwod 1993; Bjørnstad, Ims & Lambin 1999; Liebhold, Koenig & Bjørnstad 2004). While spatial synchrony has been demonstrated in many different species, from protists and fungi to invertebrates, amphibians, birds, and mammals, the mechanisms are still to be fully understood (reviewed in Liebhold, Koenig & Bjørnstad 2004).

The paper by Vindstad *et al.* (2019) in this issue of Journal of Animal Ecology first identifies three non-mutually exclusive causes of spatial synchrony. The first is the dispersal of focal species between populations, second is the dispersal of natural enemies of the focal species, and third spatially correlated environmental variation that affects population dynamics. They proceed to focus on the roles of dispersal by the focal species and environmental variation, explaining how carefully-designed studies could disentangle these effects. To understand the importance of dispersal they argue that a dispersal barrier can be incorporated into the study design, where a clear drop in synchrony across this barrier would indicate a synchronising effect of dispersal. Next, they suggest that linking spatial patterns of synchrony to wind patterns can determine if windborne dispersal is a synchronising mechanism. Lastly, by studying two species that are similar in their responses to environmental factors, but differ in dispersal capabilities they further show the importance of dispersal over environmental variation. The authors implement all these approaches using a 19-year dataset from populations in northern Norway for two sympatric geometrid (Lepidoptera: Geometridae) moth species that live on mountain birch (*Betula pubescens* var *pumila* Orlova). The larvae of both moth species disperse through ‘ballooning’ using the wind, which prompted the authors to consider effects of prevailing wind directions. Additionally, while both males and females of *Epirrita autumnata* Bkh. (autumnal moth) have wings for active dispersal, only the males are winged in the other moth species (*Operophtera brumata* L., the winter moth) (Fig. 1a). They therefore consider *O. brumata* to be more dispersal limited than *E. autumnata*. Lastly, the sampling design uses pairs of populations that span a dispersal barrier (Fig. 1b). In the study, this barrier is a stretch of open sea (of at least 1.5 km) for five pairs and for one pair it is alpine terrain, with mountains between the populations.



**Figure 1. (a) Of the two moth species studied by Vindstad *et al.* (2019), one has unwinged females (winged males) leading to the expectation that spatial synchrony for the dispersal-limited Winter moth will be constrained by dispersal barriers than the non-dispersal limited Autumnal moth that has both winged males and winged females. (b) An abstract representation of the study, showing the idea that open sea provides a dispersal barrier and spatial synchrony should be higher between more closely located pairs of populations. The white circles depict the local population in which multiple sampling points (small coloured circles within the white population circle) were used; Vindstad *et al.* (2019) used transects rather than groups of trees.**

The first main result from Vindstad *et al.* (2019) is that they confirm that spatial synchrony was stronger for the moth with both winged males and winged females (*E. autumnata*) than the moth with only winged males (*O. brumata*). They also confirm that synchrony declines with distance in both of the moth species. They explore this further by looking at pairwise correlations across all sampling levels (within and between sites) showing the drop in synchrony (correlation between populations) across the barrier was -0.21 for *E. autumnata* and -0.31 for *O. brumata*. However, they also extrapolate from distance estimates within sites to larger scales and find a discrepancy. The reduction in synchrony across the dispersal barrier is less pronounced than the authors expected from extrapolation of the distance effects observed for the within-population data (local scale); this suggests different mechanisms acting on synchrony at the local population level compared to the larger regional level. The prevailing wind direction also influenced synchrony with higher synchrony parallel to the east-west prevailing wind direction. Lastly, the authors were able to detect a travelling wave moving southwards at 50-80 km per year for the non-dispersal limited autumnal moth (*E. autumnata*) that was not observed for the dispersal-limited moth (*O. brumata*). The use of a 19-year dataset here built on previous work focusing on only one moth species for the first four years (Ims, Yoccoz & Hagen 2004), where they concluded that these populations could be asynchronous over small distances. The current study shows that this might have been due to the chosen populations being in different phases of the population cycle and highlight the difference in this data from the latter part of the longer dataset.

I was intrigued by the discrepancy between the drop in synchrony when data were extrapolated from within sites to over-sea distances compared to the observed values. I wonder if this were not so surprising due to the different sampling scales. The earlier paper by Ims, Yoccoz and Hagen (2004), presents data from within the sampled populations (i.e. for individual trees) showing that there is decreasing population synchrony between trees along their transects from distances of 0 – 1.6 km; i.e. local scale variation in these effects. Differences in leaf nitrogen content, leaf weight and leaf shape in mountain birch have been previously shown to account for more variation among individuals within sites than between sites (Karlsson & Nordell 1988). Perhaps within sites this is correlated with geographic distances along the studied transects resulting in stronger effects on synchrony. As the sampling scale is increased, the effect of individual trees could be averaged away, especially if the extent of variation in a particular trait is similar across sites. Population genetic studies on these moth species may support this idea, with *O. brumata* (the species showing stronger reductions in within-site synchrony across local distances) exhibiting genetic differentiation at the local scale (0.1-3 km) but no differentiation at the regional scale (10-40 km) (van Dongen *et al.* 1998). However, the other moth species (*E. autumnata*) did not exhibit genetic differentiation on a small spatial scale (0.6-19 km) but rather across much larger regional distances (Snall *et al.* 2004). It would be interesting to study the genetic population structure of these two moth species within the sites and across the localities that are used in Vindstad *et al.* (2019).

Finally, the results of the research by Vindstad *et al.* (2019) are also interesting from a metapopulation perspective as they test effects of dispersal among local sites and across a larger area. The observed drop in synchrony across a dispersal barrier can also be linked to the idea of limited dispersal among local populations forming a metapopulation. Spatial synchrony of local populations is detrimental to metapopulation persistence and therefore asynchrony is more advantageous in these systems (Hanski 1999); extinction processes acting on local population are often correlated due to potential synchrony of abiotic and biotic variation across the larger metapopulations, with increased synchrony at closer distances. Designing studies to understand and disentangle the causes of synchrony such as by Vindstad *et al.* (2019) can add an additional perspective to metapopulation ecology. For example researchers studying the famous Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation considered the effect of increased spatial synchrony in weather (through climate change effects) on increasing synchrony across the butterfly metapopulation, via increased frequency of drought that reduced host-plant quality and increased larval mortality (Tack, Mononen & Hanski 2015; Kahilainen *et al.* 2018). Kahilainen *et al.* (2018) explored other effects such as increased dispersal and trophic interactions with a specialist parasitoid, but only found an influence of increased weather synchrony on metapopulation synchrony. In a link to the above ideas on population variability effects at different scales, Tack, Mononen and Hanski (2015) further comment in their discussion that spatial variation in habitat variability (i.e. host-plant susceptibility to drought) at the local scale could buffer local populations against synchronous changes and increase metapopulation stability.

The findings of Vindstad *et al.* (2019) add to the building knowledge that changes in weather patterns through climate change can have strong effects on the synchrony of population dynamics across systems. Stronger effects of this might be experienced in fragmented populations, e.g. that are separated by dispersal barriers, with important ecological consequences for populations of species that have limited dispersal capabilities.

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**References**

Bjørnstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol Evol.,* **14,** 427-432.

Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R. & Liebhold, A.M. (2001) Measuring and testing for spatial synchrony. *Ecology,* **82,** 1668-1679.

Fortin, M.J. & Dale, M.R. (2009) Spatial autocorrelation in ecological studies: a legacy of solutions and myths. *J Geographical Analysis,* **41,** 392-397.

Hanski, I. (1999) *Metapopulation ecology*. Oxford Univ. Press, New York, NY.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology***,** 656-668.

Ims, R.A., Yoccoz, N.G. & Hagen, S.B. (2004) Do sub-Arctic winter moth populations in coastal birch forest exhibit spatially synchronous dynamics? *Journal of Animal Ecology,* **73,** 1129-1136.

Kahilainen, A., van Nouhuys, S., Schulz, T. & Saastamoinen, M. (2018) Metapopulation dynamics in a changing climate: Increasing spatial synchrony in weather conditions drives metapopulation synchrony of a butterfly inhabiting a fragmented landscape. *Glob Chang Biol,* **24,** 4316-4329.

Karlsson, P. & Nordell, K. (1988) Intraspecific variation in nitrogen status and photosynthetic capacity within mountain birch populations. *Ecography,* **11,** 293-297.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology,* **74,** 1659-1673.

Legendre, P., Dale, M.R.T., Fortin, M.J., Casgrain, P. & Gurevitch, J. (2004) Effects of spatial structures on the results of field experiments. *Ecology,* **85,** 3202-3214.

Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Evol Syst,* **35,** 467-490.

Robertson, G.P. (1987) Geostatistics in Ecology: Interpolating With Known Variance: Ecological Archives E068-003. *Ecology,* **68,** 744-748.

Snall, N., Huoponen, K., Saloniemi, I., Savontaus, M.L. & Ruohomaki, K. (2004) Dispersal of females and differentiation between populations of *Epirrita autumnata* (Lepidoptera : Geometridae) inferred from variation in mitochondrial DNA. *European Journal of Entomology,* **101,** 495-502.

Tack, A.J.M., Mononen, T. & Hanski, I. (2015) Increasing frequency of low summer precipitation synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary butterfly. *Proc. R. Soc. B,* **282,** 20150173.

van Dongen, S., Backeljau, T., Matthysen, E. & Dhondt, A.A. (1998) Genetic population structure of the winter moth (*Operophtera brumata* L.) (Lepidoptera, Geometridae) in a fragmented landscape. *Heredity,* **80,** 92-100.

Vindstad, O.P.L., Jepsen, J.U., Yoccoz, N.G., Bjørnstad, O.N., Mesquita, M.d.S. & Ims, R.A. (2019) Spatial synchrony in sub‐arctic geometrid moth outbreaks reflects dispersal in larval and adult life cycle stages. *Journal of Animal Ecology*.