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In this lecture we will be looking at some of the deep, biogeophysical planetary connections and how these drive change on the surface. This will take us on a journey to uncover connections at all levels, including the molecular, in the biochemistry of plant toxins, the migratory behaviours of plants and animals and predator prey dynamics. What we will explore are the ways that different types of connections help to sustain the resilience of ecosystems and how without them many species are at risk.

First let me recap on our theoretical and observational understanding of how the dynamical behaviours of living organisms affect survival and evolution. The cornerstones of ecology revolve around the predator prey cycle and the way that predation pressures change in prey populations. Classic experiments and data from the last 100 years demonstrated this coupling and its ratcheting effect. Data from the Hudson Bay trading company on Canadian lynx furs from the Mackenzie River from the mid-1800s showed a cycle with a period of 9.63 years. This was also observed in many animal populations in North Canada. The simplest explanation for the cause of the cycle was their relationship, through the food chain, to the corresponding cycle in the snowshoe hare population - the dominant item in the food of the lynx, coyote, red fox, and fisher. ¹ This relationship is known in mathematical ecology as the Lotka Volterra dynamics².

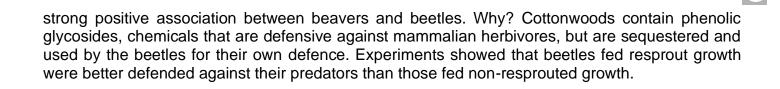
Ecologists also saw that in some systems the presence or absence of predatory species determined the entire dynamics of an ecosystem. Examples of these *keystone species* were described in marine and terrestrial systems all around the world: they either had a direct effect such as in starfish and mussels populations, or a controlling effect such as sea otters controlling sea urchins and the effect on scallops and shellfish populations along the east coast of North America. Predation is a vital and strong determining factor of connectedness in nature, sometimes working directly, sometimes indirectly.

An example of an indirect interaction is the one between beavers (*Castor canadensis*) and leaf beetles (*Chrysomela confluens*), mediated by changing plant chemistry of their cottonwood hosts (*Populus fremontii angustifolia*). ³ Resprout growth arising from the stumps and roots of beaver-cut trees contained twice the level of defensive chemicals as normal juvenile growth. However, rather than being repelled by these defences, leaf beetles were attracted to resprout growth, resulting in a

¹ M.G. Bulmer, (1974) A statistical analysis of the 10-year cycle in Canada. *J. Anim. Ecol.***43** pp. 701–715; C. Elton, M. Nicholson (1942) The ten-year cycle in numbers of the lynx in Canada *J. Anim. Ecol.***11**: 215–244; H. Tong (1990) Nonlinear time series: a dynamical system approach. Clarendon Press.

² McGlade, J.M. [ed.] (1999) Advanced Ecological Theory, Blackwell Science 353p ISBN 0-86542-734-8

³ Martinsen, G.D., Driebe, E.M., And Whitman, T.G. (1998). Indirect Interactions Mediated By Changing Plant Chemistry: Beaver Browsing Benefits Beetles. Ecology 79: 192-200.



These ideas have created a strong theoretical and modelling basis to underpin observations in many ecosystems and led to an overarching idea that connectedness in nature is linked to resilience. This is the ability of systems to rebound from sudden shocks. In addition, there is an understanding that there are fast, short cycles and longer, slower cycles involved in changes in nature. These ideas were brought together by Buzz Holling in his seminal works on Panarchy and Resilience⁴ and have helped to crystallise thinking about long- and short-term dynamics as ways of explaining shifts in nature. This has led to a search for examples in nature that display these kinds of processes and a whole field of advanced modelling including cellular automata and agent-based models.

However, there is a gap between explaining changes in the world through small sets of common variables, measured systematically in multiple locations around the world, and the findings from case studies where many more site-specific variables are measured. Whilst many of the underlying assumptions of both types of analysis are sufficient to pose simple questions, there are fundamental problems when using either one on their own for an overall interpretation. An alternative approach is to bridge the two by explicitly dealing with diversity amongst classes of attributes and configurations using fuzzy sets and logic to construct multi-attribute configurations to assess different patterns of connections in nature.⁵

Believing that this approach would be more successful in helping me understand the hidden connections in nature has driven me to undertake experiments, collect data and observe dynamical processes in different ecosystems around the world. Over the past 40 years, I have explored a range of habitats and ecosystems. Some of the places were unknown to science, others were well documented human-ecological systems. Some are dramatic, some are hardly visible. All have provided insights into understanding nature's connectedness. They are in the deep ocean and remote uninhabited tropical islands, in the highest mountains in the Himalayas, in the Arctic and the Greenland ice cap, and the Rift Valley of east Africa. Some networks are driven by powerful, planetary scale processes, others show the power of the microscopic world. All underline the connectedness of nature.

Let us start out with a beautiful butterfly – the Monarch Butterfly – famous for its seasonal migration from the United States and Canada south to California and Mexico for the winter. Monarch butterflies are native to North and South America, but they have spread to other warm places where milkweed grows. The Monarchs' colourful pattern makes them easy to identify and warn predators that they are poisonous. The poison comes from their diet. Milkweed itself is toxic, but monarchs have evolved not only to tolerate it, but to use it to their advantage by storing the toxins in their bodies and making themselves poisonous to predators, such as birds. The female monarch butterfly lays each of her eggs individually on the leaf of a milkweed plant, attaching it with a bit of glue she secretes. A female usually lays between 300 and 500 eggs over a two- to five-week period. After a few days, the eggs

⁴ Holing, C.S. (1973) Resilience and Stability of Ecological Systems. Annual Review of Ecology and Systematics 1973 4:1, 1-23; Gunderson, L. (2010). Ecological and human community resilience in response to natural disasters. Ecology and Society 15(2): 18.http://www.ecologyandsociety.org/vol15/iss2/art18/

⁵ McGlade, J.M. (2003) A Diversity Based Fuzzy Systems Approach to Ecosystem Health Assessment, Aquatic Ecosystem Health & Management, 6:2, 205-216, DOI:10.1080/14634980301467

hatch into caterpillars. The caterpillars only eat milkweed, which is why the female laid her eggs on milkweed leaves. The caterpillars eat their fill for about two weeks, and then they spin protective cases around themselves to enter the pupa stage, called the "chrysalis." About a week or two later, they finish their metamorphosis and emerge as fully formed, black-and-orange, adult monarch butterflies.

There are western monarchs, which breed west of the Rocky Mountains and overwinter in southern California, and eastern monarchs, which breed in the Great Plains and Canada, and overwinter in Central Mexico. In the east, if they emerge in the spring or early summer, they will start reproducing within days. But if they are born in the late summer or fall, they know winter is coming and so migrate south for warmer weather over distances of up to 3,000 miles. There, they huddle together on oyamel fir trees to wait out the winter. Once the days start growing longer again, they begin to move back north, stopping somewhere along the route to lay eggs. Then the new generation continues farther north and stops to lay eggs. The process may repeat over four or five generations before the monarchs have reached Canada again. In the west, monarchs head to the California coast for the winter, stopping at one of several hundred known spots along the coast to wait out the cold. When spring comes, they disperse across California and other western states.

How do monarchs make such a long journey? They use the sun to stay on course, but they also have a magnetic compass to help them navigate on cloudy days. A special gene for highly efficient muscles gives them an advantage for long-distance flight. But this still does not explain how they make the journey over multiple generations.

Sadly, western monarchs have declined by more than 99 per cent since the 1980s, and eastern monarchs by 80 per cent. The disappearance of milkweed is a major reason for their population decline. Milkweed, which is the only place monarchs will lay their eggs and the only food caterpillars will eat, used to grow in and around agricultural crops. But the systematic removal of milkweed from fields in recent years, as well as increased use of herbicides and mowing alongside roads and ditches, has significantly reduced the amount of milkweed available.

Climate change is also a concern for a number of reasons. Monarchs are very sensitive to temperature and weather changes, so climate change may affect biological processes, such as knowing when to reproduce and to migrate. There are also more extreme weather events, which negatively affect their overwintering habitats, the availability of milkweed in their breeding habitats, and their survival directly—too hot or too cold, and monarchs will die.

Meanwhile, other insects are responding positively to changes. Outbursts of the budworm caterpillar are now found on the branches of vast areas of northern pine forests. The caterpillars eat the fresh buds, setting off epic chain reactions. Inside the trees, chemical messages flow from the needle to trunk warning of the attack; within minutes every needle produces an insect repellent enzyme - a chemical defence to deter the budworm and its kin. But the message does not stop there - it pulses down to the tree's roots, then out through a hidden underground network, passing its warning to all the trees around it. This alarm bell triggers each of them to mount their own chemical defence - even trees of other species - using a 500-million-year-old social network to keep themselves, and each other, safe. Unfortunately, when the budworm outbreaks occur, they are so extensive that the forests often die within two to three years.

This connection between trees comes from the below ground microbial network of bacteria and fungi, now known as the mycorrhizal network or *wood wide web*. In the 1990s, before world of below

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ground communications was really thought about, I undertook research with one of my student's Ruth Hendry on the role of memory in forests. We studied the behaviour of a 500-year mosaic cycle in the beech forests in southern Germany⁶.

What we found was that the stress of heat stroke could cause the death of a beech tree but that without some kind of memory, the pattern in the forest was simply random. With memory included in each location the mosaic pattern emerged showing a succession of gap, birch trees, mixed forest, early beech and elderly beech. What we could observe was the dominant role of memory, which served to amplify clumping mechanisms such as radiation and early colonization and keep randomisation through death by senility at bay.

The adaptive behaviour of trees and other plants can be altered when linked to neighbouring plants by the mycorrhizal network. This can lead to mycorrhizal fungal colonization or interplant communication via transfer of nutrients, defence signals or allelochemicals. These behavioural changes in ectomycorrhizal plants depend on environmental cues, the identity of the plant neighbour and the characteristics of the network. The hierarchical integration of this phenomenon with other biological networks at broader scales in forest ecosystems, and the consequences when it is interrupted, indicate that underground 'tree talk' is a foundational process in the complex adaptive nature of forest ecosystems⁷.

For decades, selflessness -- as exhibited in eusocial insect colonies where workers sacrifice themselves for the greater good -- has been explained in terms of genetic relatedness. Called kin selection, it was a neat solution to the conundrum of selflessness in what was supposedly an every-animal-for-itself evolutionary battle. One early proponent was the legendary Harvard biologist E.O. Wilson, a founder of modern socio-biology. Wilson and colleagues showed the limitations of kin selection theory when trying to explain the evolution of eusociality⁸. According to the standard metric of reproductive fitness, insects that altruistically contribute to their community's welfare but do not reproduce score a zero. They should not exist, except as aberrations -- but they are common, and their colonies are incredibly successful. Just 2 percent of insects are eusocial, but they account for two-thirds of all insect biomass. Kin selection made sense of this by targeting evolution at shared genes, and portraying individuals and groups as mere vessels for those genes. Before long, kin selection was a cornerstone of evolutionary biology. It was invoked to help explain social and cooperative behaviour across the animal kingdom, even in humans. But kin selection is that it simply does not fit the data.

At first, eusociality was seen only in insect species whose reproductive biology enabled fertilized eggs to grow into females, and unfertilized eggs into males. As a result, sisters shared more genes with each other than their offspring. Through a kin selection lens, eusociality made sense in these species: Sisters are driven to work for each other, not their less-related offspring. But then eusociality was found in other insect species -- termites and aphids -- along with snapping shrimp and naked mole rats, where siblings were no more related to each other than to their offspring. The correlation between high genetic relatedness -- "inclusive fitness," in the kin selection argot -- and eusociality no longer held.

⁶ R. J. Hendry and J. M. McGlade (1995) The Role of Memory in Ecological Systems. Proceedings of the Royal Society: Biological Sciences, Vol. 259:153-159

⁷ Gorzelak MA, Asay AK, Pickles BJ, Simard SW.(2015) Inter-plant communication through myccorhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants*. 2015;7:plv050. Published 2015 May 15. doi:10.1093/aobpla/plv050

⁸ Nowak, M., Tarnita, C. & Wilson, E. (2010). The evolution of eusociality. Nature 466, 1057–1062 (2010). https://doi.org/10.1038/nature09205

Martin Nowak, Tarnita and Wilson exhaustively modelled this and concluded that inclusive fitness theory only applied to a small subset of all possible models. Outside of that subset, it did not work. The alternative theory, based on standard natural selection, had a twist: After starting with a focus on a single founder, selection moves to the level of colony. From this perspective, a worker ant is something like a cell -- part of a larger evolutionary unit, not a unit unto itself. Their model proved that looking at a worker ant and asking why it is altruistic was the wrong level of analysis.

The important unit is the colony. Starting out with solitary insects near to food sources, they developed genetic mutations that caused them to feed its offspring, rather than letting them fend for themselves. This progressive provisioning is widespread in insects. After this, offspring that stayed near the nest, rather than leaving would instinctively recognize that certain things needed to be done and do them. This can be seen in the real-world when two normally solitary wasps are put together; if one builds a hole, the other puts an egg in it. The other sees the egg and feeds it. The team hypothesised that this would be enough to form a small but real colony -- and from there, eusociality could emerge from an accumulation of mutations that led to a hyper-specialization of tasks, limited reproduction to queens alone and favoured the colony's success above all else. Within this colony, a queen would be analogous to a human egg or sperm cell -- a unit that embodies the whole. Worker self-sacrifice is no more nonsensical than that of a white blood cell.

In our next stop, we go to east Africa and to the Rift Valley, where I have been studying Mau Forest ecosystems including the social structure of bees. These are nurtured by the Ogiek people, one of Kenya's oldest tribes, living in the Mau Forest and other forests around Mount Elgon near the Ugandan border. The current population of Ogiek is around 20,000, divided into groups and clans. The Ogiek's way of life is based on the natural resources provided by the forest; they are hunter-gatherers and apiculturists. At one time beekeeping was carried out exclusively by men, in particular the community's elders, who were entrusted with constructing the hives and harvesting honey without damaging the trees. The traditional hives – large cylinders of red cedar (a wood resistant to parasites and the elements) – are hung from tall trees. Today women are also getting involved in beekeeping, however they manage "top bar" hives situated on the ground. The men, continue to practice beekeeping in the trees, using vines to help them climb and burning dry moss to smoke the hives prior to harvesting honey.

The life of the Ogiek is uniquely bound up with the different kinds of bees they look after in the forest. The small black African honeybees prefer the nectar produced by the *Dombeya goetzeni* plant's flowers, which gives the honey collected in August its characteristic whitish-grey colour and unique flavour. Honey harvested in December is instead slightly yellow in colour and honey from February and April varies from reddish to almost black. The different types of bees are associated with different plants and flowers: e.g. the stingless bee, *Segemiat ag Gosomeg*, that nests in the ground, *Gaposwet* known to produce sweet honey which induces vomiting upon eating, *Kipirgei* dark in colour and not aggressive, *Ng'wan* which produces bitter honey and *Somosireg*, which produces honey that is brown in colour, is aggressive and found in Sooywo. There is some evidence, talking to members of the tribe, that the different bee types can form a network across areas of the forest, communicating with each through variations in their 'waggle dance' as to the direction and distance of nectar, and possibly through chemicals. The bees are potentially connected together to behave like a *super-organism*.

Our next stop takes us to look at another type of super organism – the coral reefs around the remote, uninhabited ocean archipelago known as the Chagos Islands, in the Indian Ocean. Known to many because of the recent ruling on the removal of the population during the 1960s to make way for the

US military base on Diego Garcia, it is today one of the largest marine protected areas in the world and one which I was fortunate enough to explore during an expedition in 1996.

Why is the Chagos Archipelago so important? Because many different forms of life call it home, from the coral reefs to the various species that live on more than 55 islands. It consists of five atolls, including The Great Chagos Bank - the largest atoll in the world. Its unique habitats include 66,000 km² of shallow reefs, vast deep-sea plains and limestone platforms, as well as 86 sea mounts and 243 deep sea-knolls. The tropical ecosystem enables a kaleidoscope of wildlife to thrive. As many as 800 species of fish can be found in the archipelago, including rays, skates and more than 50 different types of shark. Around 175,000 pairs of seabirds visit the islands to breed, and the archipelago shelters populations of turtles, coconut crabs and tuna. It is also a a breeding ground for many vulnerable species of wildlife, and a haven worth protecting. Being free from the usual human impacts it represents one of our most pristine marine laboratories.

When humans first discovered the Chagos archipelago in the 1700s they introduced several invasive species including rats and cleared native forest and vegetation for habitation and the creation of coconut plantations. Coconut farming ceased in the 1970s but as a legacy of the plantation era, every island farmed for coconuts had invasive rats. By managing the abandoned coconut plantations and eradicating the rats, a more natural, seabird-driven ecosystem is regenerating, resulting in healthier islands and coral reefs and creating a refuge for native biodiversity.

Over the last decade, the archipelago has seen two significant episodes of coral bleaching due to extreme sea temperatures, resulting in high levels of coral death, and a reduction in how well the reefs function. The 2015 ocean heatwave killed 60% of the hard corals at depths of up to 10 meters across the archipelago, with some species more affected than others. For example, 86% of Acropora corals, previously the most abundant, perished⁹. Before corals were given a chance to recover another heatwave struck just one year later and data collected from the Peros Banhos Atoll showed that 68% of the remaining hard corals were bleached and 29% died, suggesting that approximately 70% of hard corals were lost between 2015 and 2017 overall.

Scientists have now discovered there is a direct link between healthy seabird populations on islands and key reef health indicators such as herbivorous fish populations. They found that seabird densities and nitrogen deposition rates are 760 and 251 times higher, respectively, on islands where humans have not introduced rats. On the reefs around these rat-free islands, fish biomass and coral reef productivity is higher, with evidence that this may also provide some resilience to coral bleaching¹⁰. Currently, over 50% of the islands, that constitutes 93% of the landmass, of the Chagos Archipelago are in a degraded state resulting in a marked reduction of biodiversity and coral reefs that are less likely to thrive. But the rat eradication is already benefitting coral reef productivity and functioning by restoring seabird-derived nutrient inputs from large areas of ocean.

Remaining in the ocean, we now travel to the west Atlantic, where I spent many years studying the behaviour and recruitment dynamics of fish populations off the coast of Canada and the USA. My job was to collected data and build models to predict the success of different species and to establish the targets for the fishing fleets. One of the commercial species I was responsible for was the semi-pelagic pollock (*Pollachius virens*). Unlike its demersal counterparts – cod and haddock – the pollock

⁹ Head, C.E.I., Bayley, D.T.I., Rowlands, G.*et al.* (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. *Coral Reef* **38**, 605–618 (2019). https://doi.org/10.1007/s00338-019-01821-9

¹⁰ Graham, N.A.J., Wilson, S.K., Carr, P.*et al.*(2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559, 250–253. https://doi.org/10.1038/s41586-018-0202-3

did not seem to fit the predator prey model or the provisioning models of recruitment success. What made pollock different to me was its reproductive behaviour which placed mature fish in the middle of the water column potentially exposing them, as well as their eggs and larvae, to a wide range of different oceanographic processes. In this sense, pollock behaviour was more like herring and sardines, but what was not clear was the extent to which predation and cannibalism determined the success of young fish to survive to the age of recruitment age. The patterns in the fishery suggested otherwise. We did not know where pollock spawned but looking at the physical world in which pollock eggs and larvae could emerge made me look not only at the small-scale oceanographic processes but also the large-scale ones. The largest of these in the region is the Gulf Stream. Its fast-moving waters move large pelagic species such as tuna and swordfish and sharks on long journeys from the Caribbean up to the northern waters and across the Atlantic to the east. Remote sensing imagery had just begun to be available and so I projected the movement of the Gulf Stream and the eddies spinning off, to see if there was any spatial correlation with the pollock populations. There was more than a hint that this was the case. So, armed with a model and a sea-going research trawler I went to sea to find out if my hypothesis was right. If we found mature fish in or near gyres and eddies that were tracking offshore, then in 2 -3 years' time, recruitment success would be low. If we found mature fish in eddies tracking onshore, then the prediction was that recruitment would be high. We tracked the eddies, and our first success was to find pollock spawning in the waters of a series of eddies spinning off the Gulf Stream along the continental edge. This time they were caught in the onshore movement. My prediction was that in 2 years' time, the pollock stocks would be positive. This was the first time an early detection system had been used and it proved to be successful. Subsequent surveys showed that the mere physicality of the ocean was enough to determine the annual fluctuations.

Deeper under water along the edge of the continental shelf at more than 1500 metres, lies a world of canyons and wide-open spaces. In successive research surveys we found different species were concentrated in different areas with very little overlap. In the Carson Canyon we found the only major concentrations of surf clams, to the north were the northern shrimp. Even more interesting was the discovery of recovering populations of halibut. In the early 1990s, the Northwest Atlantic Ocean underwent a fisheries-driven ecosystem shift. Even today the iconic cod (Gadus morhua) remains at low levels, while Atlantic halibut (Hippoglossus hippoglossus) has been increasing since the mid-2000s, along with an increasing interest from the fishing industry. Knowledge about halibut ecology remains limited, and the lack of recovery in other collapsed groundfish populations has highlighted the danger of overfishing local concentrations. Looking at the spatial structure of juvenile Atlantic halibut over 36 years and three fisheries management regimes, it has been possible to characterize the persistence (similarity of spatial structure over time), connectivity (coherence of temporal pattern over space), and spatial variance (variation across the seascape)¹¹. Two areas of high juvenile abundance have persisted through three decades whereas two in the northeast are now diminished, despite the increased abundance and landings throughout the management units. The persistent areas are neighbouring and overlap with full and seasonal area closures, which suggetse they may be refuges. Connectivity was estimated to be 250 km, an order of magnitude less than the distance assumed by the definition of the Canadian management units (~2,000 km). This smaller ~250 km scale of coherent temporal pattern suggests that there is a much more complex population structure than previously thought.

Further to the east on Kalaalitt or Greenland, I spent 10 years exploring and mapping some of the largest impacts of climate change on earth. The surface of the ice is littered with blue lagoons of

¹¹ Boudreau SA, Shackell NL, Carson S, den Heyer CE. Connectivity, persistence, and loss of high abundance areas of a recovering marine fish population in the Northwest Atlantic Ocean. Ecol Evol. 2017 Oct 18;7(22):9739-9749. doi: 10.1002/ece3.3495. PMID: 29188005; PMCID: PMC5696389.

melting water, as summer temperatures rise as high as 26°C. But it is the impact on nature in this natural deep freeze which is interesting. Polar bears, seals, narwhals are all affected by the melting sea ice. My Inuit tracker said that looking at the melting ice was like the "melting of his heart" – he felt it so deeply. The impact on animal life couldn't be clearer. Historically, the local hunters would be given a licence to hunt a polar bear; because it is so dangerous only one or two men would set out on the hunt. But as the ice has begun to melt these hunts are becoming fruitless.

But now along with the melting sea and land ice is the growing evidence of the impacts of pollutants being transported into the Arctic via air and ocean routes. Agricultural chemicals including organochlorine pesticides used in Europe (and not in the Arctic) are present in Arctic air, water and snow, and in animals and humans at levels that give rise to considerable concern. New contaminants — such as flame-retardant chemicals — are now being detected in the Arctic and their effects on different species and on the environment becoming apparent. Alien species are also appearing, such as King crabs, following the new shipping routes opening up.

Everywhere around us are examples of how the connections we see in nature are demonstrations of the deep ways in which life on earth is connected through microscopic up to planetary processes. In the next lecture we will explore these further. What I have tried to show in this lecture is the vast diversity of connections between organisms themselves – many of which we are still trying to understand. Exploration can take the form of journeys to remote and uninhabited places, but even within your immediate environment nature's connections can be a fascinating world of enquiry.

I want to end in a place where we can still get a picture of what Europe was like hundreds of years ago. The Białowiecża Forest UNESCO World Heritage site, on the border between Poland and Belarus. It is an immense range of primary forest including both conifers and broadleaved trees covering a total area of 141,885 hectares. Situated on the watershed of the Baltic Sea and Black Sea, this transboundary forest is exceptional. It is home to the 30% of the world's wild population of the European bison and one of the largest areas of old growth forests characteristics of the Central European mixed forests terrestrial ecoregion. A consequence is the richness in dead wood, standing and on the ground, and consequently a high diversity of fungi and saproxylic invertebrates. There are 59 mammal species, over 250 bird species, 13 amphibian species, 7 reptile species and over 12,000 invertebrate species. Most important are the large number of complete food webs including viable populations of large mammals and large carnivores such as wolf, lynx and otter. It is here that we observe how connectedness in nature is what gives it resilience and adaptability.

Let me leave you with a film I made while at the European Environment Agency as part of a series of short documentaries called the Environmental Atlas about Europe¹².

As the Park Warden Martin says you do not need to know everything to see the beauty.

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¹² https://acefilms.tv/filmpage_adayinmyforest/