Seminar Diary

* Write a half-page on 10 seminars and create a “seminar journal”.
* Due: 1st July 5pm, email pdf to Samraat.
* The diaries are not assessed for beauty of prose or scientific rigour, but on the basis of how good the logical structure of the entry/account for each seminar is.
* Please do not exceed 1/2 page per seminar's entry/account.

Model Examples

Adaption to Environmental Change in Communities of Aquatic Microbiota

12/10/17 - Dr Etienne Low-Decarie - University of Essex

Organisms are fundamentally driven towards fulﬁlling particular ecological niches, extreme or otherwise. If we understand and can quantify the niche that a particular organism is adapted to we can predict not only its location and range, but also its potential ranges and tolerances to change. However, diﬀerent models can predict wildly diﬀerent niches, and are often speciﬁc to the particular dataset they were developed from/for.

Low-Decarie et. al used lab experiments along with Amplifying Bioreactors (ABRs) to evaluate community rescue and extremophile abundances. When communities are exposed to sub-lethal levels of stressors prior to exposure to typically lethal doses, they can often recover to pre-stress states. This recovery is dependent on the diversity, disparity, dispersal, and level of sub-lethal exposure. Highly adapted organisms survive well in benign conditions, however as stressors (such as pH or temperature) are increased, adapted organisms fare better. Overall adaptations to benign changes are less likely than adaptations to sub-lethal stressor changes.

Impacts, Spread, Evolution and Virulence of “Frog Ebola” Viruses

19/10/17 - Dr Stephen Price - UCL

Ranavirus is an emerging infective disease that aﬀects all of the 6 major UK amphibians. It damages individuals at all life stages, and can spread past amphibians. Price et. al showed that salamander pets are a likely source of pathogen pollution, with frog and salamander farms in China acting as disease incubators. To assess the spread of disease through the United Kingdom, they started an ongoing frog mortality citizen science project. In addition to live data, Price carried out in vitro experiments to test the viability of temperature as a predictor of ranavirus status. FE3-like strains of ranavirus were particularly well-adapted to high temperature (shown later in vivo)

From genomic analysis, ranavirus seems to have a signiﬁcant variation in terms of genome arrangement and content. The genome has undergone widespread gene recombination and horizontal gene transfer, and is currently undergoing positive selection.

Seminar One

Deep-time evolution of biological responses to temperature changes

Dimitrios Georgios Kontopoulos

10th October 2019

* What is the topic?
* Why is it important?
* What experiments/investigations have been done to learn more about this topic?
* Any conclusions?

Species at risk from climate change, one of the major threats to global biodiversity today. If we are to better forecast how different kinds of species will respond to climate change we need to develop a thorough understand of how physiology responds to temperature change over shorter or longer time scales. One way of looking at that, is to look at how biological traits respond to temperature changes. If you measure biological trait such as growth rate or photosynthesis or respiration, if you measure these at different temperatures you typically get this unimodal curve. So, this curve is called the thermal performance curve. Trait values typically slowly increase with temperature until an optimum temperature (which is called Tpk) they steeply decline. The maximum height of this curve is called Bpk, and it’s a measure of the performance of the organism. Understanding how these curves vary between different individuals, populations or different species is important because for example we know that interacting species tend to have systematic differences in those kinds of curves and if we know the processes that generate variation in these curves then we can better forecast what will happen under different scenarios.

Throughout this talk I will be using this mathematical model, the Sharpe-Schoolfield model, to quantitatively characterise different aspects of the shape of these curves. As you can see the numerator of this model is just an araneous equation and captures how smoothly the curve rises until the thermal optimum. Whereas the denominator captures how steeply the curve declines about the optimum. The basic assumption of this model is that the biological traits of growth rate here is being determined by the effects of temperature on the activity of a single rate limiting enzyme. So, this rate limiting enzyme is deactivated at very high temperatures whereas at low temperatures it operates at very low rates because of low kinetic energy. This model can be considered as mechanistic but you can also use it as a phenomenological model just to capture the statistical relationship between trait performance and temperature. This model has four main parameters, Tpk –thermal optimum, E – captures how smoothly the curve rises up to the optimum, a measure of thermal sensitivity near the range of temperatures in which organisms typically operate. Ed – captures how smoothly the curve declines after the optimum and then B0 – which is approximately the trait value at a low normalisation temperature. After getting estimates of these four main parameters we can also estimate two more parameters: Bpk, the maximum height of the curve, and Wop, the difference between the thermal optimum and the temperature at the rising part of the curve where the performance is half of the maximum (operational niche width), another way of looking at thermal sensitivity. Both E and Wop are measures of thermal sensitivity. For this reason we would expect them to be correlated, so imagine you have a very steep slope of the rising part, then by definition your niche width would necessarily become narrower (Wop would become smaller).

At this point I’d like to introduce the Metabolic Theory of Ecology, which is arguably the most popular macroecological framework. It makes a lot of explicit predictions regarding how these curves, and also other macroecological patterns, will vary with temperature. So, the metabolic theory has been used mostly for large-scale comparisons of trait performance for example across multiple taxonomic groups, but very few people have looked at what these predictions hold when you look at within species for example or when you look through evolutionary time. So, my goal throughout this PhD and this presentation is to understand whether the predictions of this framework hold when we look at the evolution of species.

In my talk I will tell you about how thermodynamic constraints influence the shape of thermal performance curves. How thermal sensitivity evolves and near the end I will tell you a bit about what we can do to link those kinds of approaches with other fields and other search traditions to develop a thorough understanding of thermal adaptations from multiple ecosystems.

For the first part if we look at the literature for hypothesis of thermal performance curve evolution, we find that a lot of different hypothesis that can be broadly placed along the continuum that ranges from strong thermodynamic constraints to weak thermodynamic constraints that can be at least to an extent be overcome by adaptation. So, at the strong thermodynamic constraint extreme we have ‘Hotter-is-better’. So this hypothesis assumes that due to very strong thermodynamic constraints these curves can only differ in the thermal optimum, the maximum performance and as you can see the vertical lift is the same for all these curves and the slope of the rise is the same. So, in this hypothesis we expect a very strong positive correlation between the thermal optimum (Tpk) and maximum performance (Bpk). This hypothesis basically assumes that at higher temp the activity of the underlying enzyme is accelerated because of the higher kinetic energy and this is why they would get an increase in the max performance.

If we relax those assumptions then we get to a ‘Weak hotter-is-better’. Where we either have variation on the vertical lift of these curves, variation in the slope of the rising part or in both. So if we assume that the vertical lift of the curves vary, then this is very close to what the metabolic theory of ecology expects.

The metabolic theory of ecology suggests that variation either here, at the offset, or at the max height, is associated with body size. So, imagine that you have a v high body size therefore you need to invest a lot of energy into maintaining it, therefore this leaves you with a lower maximum performance and vice versa. Small body size = higher max =energy to increase max performance. So in this case we would have a weak positive correlation between thermal optimum (Tpk) and max performance (Bpk).

Next, moving towards weak thermodynamic constraints we have the specialist-generalist hypothesis. This hypothesis assumes that for species to achieve a very high trait performance they need to become thermal specialists. So they need to operate at a very narrow range of temperatures, whereas if you are a thermal generalist and you need to operate over a wide range then you would have to pay a metabolic cost and this would decrease your maximum performance. So in this case we would have a negative correlation between Bpk and Wop.

And finally the last hypothesis is the perfect biochemical adaptation hypothesis which suggests no matter which environment a species is found, adaptations should be able to maximise its Bpk. All species would have the same maximum Bpk, across different enviros.

To test this hypothesis we need to look at two things, the correlations between thermal response parameters and understand how some of those parameters, how they offset the slope of the rise or the maximum height, how these parameters evolve across species, what is the kind of variation across species?

My approach was to take a phylogenetic comparative approach and examine the correlation structure of these parameters but also examine the phylogenetic signal of its parameters separately. So basically the phylogenetic signal is the measure of whether close related species have more similar trait values than species chosen at random. If, for example Bpk is held constant, then it should vary like random noise across species and it shouldn’t exceed the phylogenetic signal. Currently we have big databases of thermal performance curves where we can examine these questions and answer these questions.

My data comes from the literature. They are phytoplankton growth rates. Typically, people go to the environment, isolate the strain of phytoplankton, take it back to their lab and grew it under a range of temperatures under light and nutrient saturated conditions. Before measuring the growth rate at every temperature, we first allow the species to acclimate. What I did was I took all of those data and feed the model to each species or strain separately. This allowed me to obtain estimates of the thermal performance parameters for each species/strain. To analyse these, I feed it a phylogenetic regression model where I estimated the covariance structure of four thermal response parameters, controlling for the phylogeny of the species and local environmental effects – temp variation and habitat. By doing that I managed to identify two correlations between thermal performance curve parameters. One was between the two measures of thermal sensitivity, a negative correlation between the slope of the rise and the operational niche width which is what we expect to find. The other correlation was indeed a weak correlation between the thermal optimum and the maximum performance. As you see here, as temp increases (the thermal optimum), the max performance of species weakly increases as well. However, if you just discard these three data points here, then this correlation is no longer significant. This means that most of this pattern is driven by species at low temperatures. There is an increase then it levels off. These results are consistent with a very good ‘hotter is better’ pattern.

The next thing I did was I measures the phylogenetic signal for these parameters and you can see it here. The phylogenetic signal or phylogenetic heritability ranges from zero to one. You see that all of these parameters have at least some amount of phylogenetic signalling. The strongest amount of signalling is in the thermal optimum which evolves fairly gradually across species. Whereas some other parameters may make larger jumps in parameter space. These results all tell us that there is variation in the intercept and the slope of the rise and there is also variation in the maximum performance. The final thing to test this hypothesis was to look at the effect of body size so I obtained estimates of cell volume and I looked at whether these correlate with the offset of the curve or the maximum height of the curve. The result is the only significant correlation was the max height of the curve. As cell volume increases the max height of the curve weakly declines. Cell volume explains 15% of this variation and if we add species identity in there then this gets all the way to 72% of the variation being explained.

These results tell us 1) the max performance weakly increases with the thermal optimum. Some of this variation is driven by cell volume, but there is variation in both the intercept and the slope so with all this in mind we can say that phytoplankton thermal responses are broadly here nearer to weak thermodynamic constraints.

Next, we will focus on thermal sensitivity. A big debate in the lit. The metabolic theory of ecology suggest thermal sensitivity should not vary across species due to thermodynamic constraints. It should be almost held constant. However, I found that there is some phylogenetic signals in this parameter. In 2011 this paper came out – Systematic variation in the temperature dependence of physiological and ecological traits – it looked at thermal sensitivity across a large variety of species and different traits. They found that thermal sensitivity is not fixed, it has a distribution. This distribution isn’t gaussian. It has a long tail towards high values. They found some evidence that prey traits may have lower thermal sensitivity that predator traits. They called this the life-dinner principal. Prey traits should be under stronger selection for being less dependent on temperature than predator traits. Even in this paper there wasn’t a clear evolutionary explanation on how this variation came to be given that we expect thermosensitivity to be fixed because of thermodynamic constraints. In this project we would like to test two hypothesis regarding the evolution of thermosensitivity. The first hypothesis agrees with the metabolic theory of ecology and it is that thermal sensitivity evolves around an optimum value. This value is set because of thermal dynamic constraints. Occasionally some species are able to break free from those constraints and maybe have variation in thermal sensitivity but because of selection, other closely related species will move very quickly back to the optimum value. The second hypothesis is that thermal sensitivity may evolve in other ways. Maybe there is a global optimum but its attraction is very weak. It allows species to explore a v wide area of the parameter space around it. Or maybe certain clades have a higher rate of evolution in thermal sensitivity and better able to explore the parameter space.

To test this hypothesis, I used the phytoplankton growth rate dataset but also another dataset of prokaryote growth rates. First, I examined how the variation in thermal sensitivity is distributed along the phylogeny. This method allows us to differentiate between random evolution between an increasingly overlapping parameter space of different lineages and between a segregation of lineages with the parameter space, similar to adaptive radiation. Here on the x axis we have time, 0 is the root of the tree, 1 is the present time. Here (y-axis) is the mean clade disparity in thermal sensitivity. These shaded areas are the expected disparity line that we would get from 10,000 simulations of random evolutions. If a trait was evolving randomly on our tree, what it’s disparity would be. If our actual disparity line is above shaded area then this means lineages overlap in parameter space. If it is below then different lineages occupy distinct areas of the parameter space. We calculated the disparity line and we found as we move towards the present we have an increase in overlap in the parameter space by different lineages. Species that come from very different clades may have v similar values of thermal sensitivity. This suggests that it’s not the evolutionary history that matters that much, it’s that the environment selects for particular values of thermal sensitivity. No matter what clade you are from you can adapt.

You can see better if we look at the major phyla in this analysis. There are the main phyla. You can see that for example Dinophyta and Cyanobacteria are very far away from each other in their phylogeny but they have similar distributions of thermal sensitivity.

We tried to see if different clades vary in their rate of evolution of thermal sensitivity. We mapped the rate of evolution on each different branch of the phylogeny. High rates of evolution shown in red/brown. Pattern is very patchy. No one particular clade with high/low evolution of thermal sensitivity. All over the phylogeny we get random bursts of trait evolution of thermal sensitivity. Leads to the pattern we saw before. To better understand the results, I performed a visualisation of the thermal sensitivity evolution. Time (x-axis) and values of E (y-axis) Yellow lines are median estimated values of thermal sensitivity, red areas are confidence intervals. As we move from root to present there is an increase in range of trait values. There is not one global optimum, but species are able to explore the parameter space. When we saw this result we said okay this is population growth rate, it is a relatively higher order trait and maybe there are a lot of processes going on. What would happen if we looked at different traits that are closer to the physiology. I tried to do the same analysis with lower physiological traits, such as photosynthesis and respiration of algae, aquatic and terrestrial plants and the data sets were a bit smaller but the results were pretty much to same. We can see the thermal sensitivity even for those traits. Typically explores a wide area of the parameter space and can vary a lot even between closely related species.

All these results suggest thermal sensitivity responds to selection. It’s not just fixed because of thermal dynamic constraints. Nobody else has shown how thermal sensitivity may vary across different environments across such a macroevolutionary scale. One thing we would expect would be that thermal sensitivity should vary with latitude. Near the equator you would expect selection for thermal specialists with very high values of thermal sensitivity. As we go to middle latitudes we would expect increasing selection for thermal generalists because of the variation of temperature with latitude. What I did was I took the thermal sensitivity values of all those traits, population growth rate, photosynthesis and respiration, and I tried to see if they all varied with latitude. The result is exactly as we would expect. You find high values of thermal sensitivity at the equator and as we move away we get a decrease in thermal sensitivity.

Latitude and trait identity explain 23% of the variation in thermal sensitivity and when we add species identity we get to 58% of the variation being explained. The traits have different intercepts but the same slopes for latitude, but this may be a fact of the small sample size. This result hasn’t been shown before because the metabolic theory of ecology assumes that thermal sensitivity is fixed across species.

I’d like to tell you about how we can take these kinds of approaches and link them to our other levels of organisation in order to develop a more unified picture of thermal adaptation. So when I think about the effects of temperature on biological systems I don’t just think about biological traits. I tend to think temperature affects all levels of biological organisations. Here is a simplified version of a community of three species interacting. Each species is composed of a population. Each pop has individuals. Each individual is composed of different cells and tissues. Each cell has a copy of the genome, mitochondria that produce energy and also expresses proteins. Temperature effects every single thing on this figure. It affects probably genome composition, amino acid composition in proteins, how different species interact with each other. Most frameworks tend to focus on one particular level of organisation. Then they assume that levels below or above tend to fall apart. Whereas my argument is that if we are to develop a thorough understanding of how organisms will be affected we need to embrace all of this complexity and understand how temp affects each level separately and hwo they interact with each other. One approach that we could follow is to get some ideas from the complexity science field. For example, we can assume that each level of biological organisation is a complex system which is composed of agents. A gene within a genome can be its own agent and respond to temperature and other genes in different ways. By doing that we will be able to predict properties of those systems that can’t be identified by studying each agent in isolation. Obviously this is no easy task and this is a very long in the future idea. What we can d for now is we can look at different pieces of the puzzle and see how they respond to temperature.

Besides physiology I looked at how temperature affects the effects of mutations. Here on the left you see a protein stability curve with temperature. Mutations tend to decrease the stability fo the protein. Conventional assumption in lit is mutations should have same affect regardless of temperature. Whereas from biophysical pov we would expect that mutations would be more detrimental at higher temperatures. Imagine a thermophilic enzyme. If a mutation happens there, because of the high energy of protein atoms, then this mutation would strongly destabilise the protein. Wheras if we lowered the kinetic energy of those atoms the effects of this mutation wouldn’t be so sever. We expect mutations would be more detrimental at high temp, implications for the rate of evolution at those temps. I used adenylate kinase, this is an essential enzyme, found in all organisms, it catalyses an essential biochemical reaction. I got seventy structures of this enzyme from bacteria and archeae. I then divided them into thermal groups, psychrophiles, moderate temperatures, thermophiles. Then I performed molecular dynamic simulations, biophysical simulations, put this enzyme under a forcefield surrounded by water molecules and some salt molecules. You simulate how this enzyme moves in the solution under the temp that’s close to it’s environment. Finally, once you do those simulations you can extract confirmation of these enzymes, see how they move, find conformational structures. Take those confirmations and submit to server that performs all possible mutations. It tells you what the mutations would be like, beneficial or detrimental. Results showed that mutations become more destabilising with temperature.

I then wanted to see if these results hold if we look within species. I took five species and performed these biophysical simulations at multiple temperatures. You get a similar relationship within species, although there is a change is shape of the relationship. These results suggest that mutations become more detrimental to proteins stability both within and across species. Like I previously said, we would expect these to have some implications for the rate of molecular evolution trait temperatures. So using this I build a phylogeny using 44 genes for those 70 species and then I allowed each branch of this phylogeny to have a different rate of molecular evolution, a different substitution rate. By doing that I was able to get substitution rates for those seventy species. I corrected those substitution rates for generation time and tried to see whether you see an effect of temperature. There is a strong relationship between temperature and substitutions. This suggests that at higher temperatures substitution rates are lower, possibly due to lower mutation rates or effective population size. It’s a result that people haven’t shown before. There is v weak evidence that when you move to higher temp your mutation rate may decline, but few studies have looked at that, and only a few species. Result is very interested for another reason, it is completely opposite to what the metabolic theory of ecology predicts. It predicts that at higher temps you would have high rates of molecular evolution because you would have a higher production of oxidated free-radicals that would lead to mutations.

This is another point in m argument at least that we need to embrace all of the complexity, not focus on one particular level like metabolic theory does.

Other things to be done in the future: look at the genetic basis of thermal response curves. We don’t really know what drives shift in thermal optimum, what drives shifts in thermal sensitivity at the genetic level. One way someone could approach this would be to grow different strains of the same species at multiple temperatures. So you get thermal performance curves for a lot of different genotypes for the same species. Then using a genome wide association study, identify the genetic drivers of variation in all those different thermal response curve parameters. Other things that could be done would be for example to see how these species interact and whether these interacts are driven by temperature and whether such variation is also associated with changes in the physiological and other levels.

The take home message from this talk is that contrary to what we would expect from the metabolic theory of ecology, thermodynamic constraints have a very weak influence on the shape of thermal performance curves. The various TPC components evolve in different ways (e.g. gradual vs non-gradual exploration of the parameter space). Mutations become more detrimental to protein stability as temperature increases. Linking approaches from diverse fields and research traditions is key for developing a unified picture of thermal adaptation.

Seminar Two

A manifesto for systematically describing consumer-resource interactions

Daniel Barrios-O’Neill, Leverhulme Trust, University of Exeter

31st October 2019

**picture of log** Why is it in the open ocean, fish associate with the only habitat structure available to them?

Study functional responses. Everyone has a two liner about why functional responses or what they study matters. Everything that is interesting and consequential in ecology turns on the capacity of organisms to survive and grow and reproduce and that turns on their ability to acquire resources. Consumer resource interactions are at the heart of ecology. The currency of ecology. That’s why they are worth quantifying.

Consumer-resource interactions. Pac man consumes resources in proportion to the rate that he encounters them. He has no handling time. That produces a relationship between the prey/resource density in the enviro and the consumption of that resource that’s linear. A type 1 functional response. But, we all at some point have to spend time handling our food resources. We have to ingest them, we have to digest them. This limits the rate at which we can consume resources. Leading to a saturating relationship – type 2 functional response. Third type – type 3 – effectively describing the same phenomenon but with an inflection at low resource densities, to reflect things like learning.

In terms of the way we fit data and model these functional responses, there are two quantities to keep in mind. The attack or space clearance rate or capture rate, and the second is the resource handling time. Useful heuristic for describing two parts of the function resource curve along that gradient of resource density. You can think of capture rate as containing some information about the space through which consumers and resources move. Info about the physical world. Handling time is limiting resource consumption at high densities because it relates to biomechanics to some degree, to physiology and metabolism.

Size and temperature define a lot across the biosphere. Roughly speaking, larger animals and warmer animals have higher attack/capture rates and shorter handling times. Warmer and bigger = eat more. Metanalyses: 1000-2000 data points, not much. Distribution among marine, freshwater and terrestrial systems, highly skewed. Marine systems underrepresented. Sudo replication in data. Currently limited position to be able to say anything meaningful.

Differences in taxonomic groups. Placeholder for strategy. Collected lit on marine benthic consumers. An underrepresented broad group. I’ve augmented what I could find in the lit with new experimental data, to target underrepresented groups, like obligate sit-and-wait predators. You can consider that organisms adopt either active encounter strategies, they more around the find resources, or they sit and wait for things to come their way. You can consider these to be categorical predictors of some of those patterns in the previous slide. Taxon is kind of opaque to changes in strategy. A crab could employ several strategies. If we describe just in terms of taxonomic groups we don’t necessarily get all the useful information about changes in strategy which can happen moment to moment in real terms.

So, when you put all that data together what you get is highly skewed results. There are lots of data for the active static group, for the active mobile group, for filter feeders. Literally only two of three data points for marine benthic grazers, deposit feeders and obligate sit and wait. The overall pattern is filter feeders have lower size specific feeding rates than those other key groups. That’s a pattern that warrants some kind of explanation.

Mutual interference. This is something that has occupied many lines of papers, particularly in 80s and 90s. A debate that continues. Idea is that as the density of predators foraging on a patch increases, the per capita rates of consumption go down, this is mutual interference. The fact that this occurs is almost unambiguous, although the effects are subtle. The best models to describe it have been the focus of a lot of the debates, whether we should use ration or prey or predator dependent models. My position on that whole thing is that it is a little bit academic and here’s the reason: this is a recent paper looking at Ostracods, going from one predator to four predators and these are the per capita functional responses. The first thing to note is that the difference between per capita functional responses in one and four are extremely subtle. Not statistically significant. You can barely see, but the competing models, largely predict the same thing. In terms of consequences for energy flow, consequences for stability of populations, this seems like something of a side point.

A better question to ask about interference might be something like, is there a size bases for understanding interference? Does interference scale with bodysize? I’ve been trying to address that question using reasonable large datasets. Three sizes with crabs, crosses with 3 sizes of mussels, crossed with 3 densities of predators. From that data you get quite a subtle effect as the number of predators increases, the scaling with body mass ratio flatterns out. The data is really messy. This demands, three to four times as many data points. If we want to ask meaningful questions about the scaling of interference, we can’t do it without doing the experimental work.

Thinking on about patterns which aren’t necessarily grounded in size and temperature but are generalisable. This is a pattern of Samraat’s, influential because my take home from this is, well here’s a generalisation that we can make about consumer resource interactions across species and systems which has a size basis but is fundamentally about the physical space in which consumers and resources interact. That is a pattern that is just sat there in the data and there’s a mechanism underpinning that. Consumers that move and forage through volume tend to encounter each other more frequently than consumers that forage over surface, so that leads to a slightly steeper scaling relationship of those feeding interactions. It suggests to us that encounter rates are important for improving our understanding. We need to start thinking about the interaction space to improve our understanding.

I’ve been trying to do that a little bit with this big marine meta-analysis. I’ve been developing agent based models that basically assume that consumers and resources that move, go on random walks, at velocities that scale with their size, that they have reaction distances and detection regions that also scale with their size. And then just asking, basically, fully empirically parameterising these models with the prey density and prey size data from that data set of marine benthic functional responses. The questions that I would have, given what we know about the strategy and the movement of these consumer resource pairs and essentially the biomass density of resources of resources that they’re going after, are there any hard limits to the rate at which these different strategies can expect to encounter resources before anything else has happened, before any attacks have happened. I’ve been doing that in NetLogo.

When you look at consumer mass and you look at resource biomass, rather than units, it’s obvious that at a first pass filter feeders cannot encounter as much resource biomass as other strategies. Seems like a trivial result. However, when you consider that result in the context of how we think about filter feeders in the literature, it is interesting because this is what you see in the classical lit, this is how functional responses are presented. Type 1 pac man, feeding optimally. Epople talk about the adptive significance of filter feeding as a strategy because of the difference between type 1, 2 and 3. The problem with these kinds of analyses are, they bring together lots of different type of filter feeders (whales and daphnia). Whales swim to exploit concentrations of resources, different to being stuck in one place and having to accumulate resources in the environment come what may. Fundamentally a filter feeding that is static is more akin to something like a tree than a filter feeding that moves through the environment to exploit concentrations of resources.

Habitat Structure. Back to the log. Thinking about movement through space. This log, things accumulate round it. Like a stone in your garden, things crawling. The physical structure of the world is consequential to species survival. What we need to do is get to a position where we understand from first principals how physical structure modifies those encounter rates and modifies interactions, without being qualitative about it.

Looking at this since PhD. This is a piece of work, big piece of experimental work, where I took an invasive corophid arthropod you can find drifting in the water column, you can find established in a simple habitat or in complex habitats. 3 different contexts for potential predators to forage for this prey. My approach here was to try and get as many animals as possible. This is the largest stand-alone functional response experiment. Going from very large to small animals, across several orders of magnitude. Exposing them to three different experimental contexts. They are three dimensional swimmers, with three dimensional interactions. With substrate they settle. Not a neat test of dimensionality because when they settle their behaviour changes. My question is, how does this foraging context alter the scaling of the feeding interactions of a potential community of predators.

It’s worth noting, that although we expect positive scaling of capture rates with consumer size across the biosphere, we find hump shaped things across the global trend, and that is because essentially, consumers that forage for relatively small resources and those that foraging for relatively large resources, forage sub-optimally.

When you look at the drifting 3-D content you find that hump shapes distribution. This is log predators prey mass ratio plotted against capture rates. When you look at the simple and complex habitats, you see a collapse in that hump shaped distribution. My take is this, these are large differences in capture rates that are potentially occurring over v small spatial scales. When you consider that as compared to all the work that’s been done on interference, those differences are subtle. If this is a characteristic of interactions in other systems, then we’d like to know about it. This is fundamentally going to change the outcomes of any models that you might wish to parameterise. In particular the strongest interactors, do the work relative to their position in the drifting context.

Interactions are ‘Context-dependent’ this is an experiment where I’m doing a functional response in situ with shrimp that are migrating up and down a lake water column. I’m taking them and doing experiments in situ, in shore and off shore, on the surface, on the bottom, in the day and in the night. You can see that the attack rates and handling times change a lot. As organisms move through the world, these interactions with their resources are always changing depending on the context in which they forage.

A wider take on why the physical structure of the world matters. We are changing it, in a lot of ways. We are introducing complex habitats, where before there were none. We’re changing structure in ways that we don’t understand the consequences of from first principals. We need to get to a position where we understand the effects of habitat structure in first principals.

Parsing habitat structure. When we do these experiments we do reference treatment, then single unit treatment, then double unit treatment. This covaries lots of things at the same time, volume, surface area, potential for camouflage. We can measure the overall effect size of changing context. We cannot ascribe easily the reason for the changes. To do that we need to get away from assuming working with natural structures is the best thing to do. Need artificial structures to precisely manipulate space/structures in known ways and scale those manipulations so that we can test specific hypotheses.

Increasing predator-free space. Reef schematics. Moving from left to right, increase in predator free space/refuge space. Manipulating refuge space and maintaining surface area and volume of system. Certainly, better than throwing mussels on a bucket. Magnitude of functional response changes as well as shape, along that gradient. Change along continuous, quantifiable dimension of habitat structure. Fractal dimensions of these habitats are all the same. Don’t necessarily tell us anything useful about the space in terms of how consumers and resources might use it.

Consider another dimension of habitat complexity, for example, how the density of obstacles in an environment might affect an interaction. You need to be very precise about how you change structure. Errors lead to the creation of refuge space, can’t isolate effects. 3-D printing! V precise, scale the system. Resin good for printing small scales. Printing time scales with length. Minutes to hours to days. Generating lots of data about structure!

Process: Agent based models > 3D habitats > experiments > interpretation > model fitting.

Beyond size, available data limits what we can know: metabolic predictors are well established. Model species and systems skew limited global data. Modifiers of encounter rates are key. Structure cannot be understood without new data.

Down with model species and systems! Crabs and mussels only going to cut it for so long. Lacking data points for important, underrepresented groups. Address knowledge gaps.

We need to get Linnaean! Being arbitrary at the moment. When we do these experiments, we need to know all the variables in ways that other people can use. We’re not consistently doing that.

Opportunities to harvest data are myriad. E.g. cameras on the backs of turtles. New pipelines of data.

Open access data and open source tools.

Ecologists are legion. More ecologists working today that 50s and 60s.

Undescribed interactions are as exciting as undescribed species. Treat interactions and knowledge gaps as something to be discovered.

Seminar Three

Flowers, bees and shifting seasons – how to adapt when Nature’s calendar goes out of sync in a warming world

Jacob Johansson, Theoretical Population Ecology and Evolution Group (The PEG), Lund University, Imperial College London

21st November 2019

I want to talk about flowers and bees and shifting seasons and how they adapt when Nature’s calendar goes out of sync in a warming world. Background to this is as you may be well aware of many biologicals events now occur earlier. In the last decades we have seen big shifts. Flowering times, bird migrations, butterflies appearing earlier. Well establish examples. Another pattern we also see if the large variation in rates of change among species and events. Some species have shifted a lot, others appear not to be shifting, other going in the other direction. Question is how do we interpret these patterns? Are these responding strongly, are they doing well? Those that don’t respond doing less well?

One of the big fears is called phenological mismatch. Phenology is seasonal timing of biological events. You do your thing, reproduction/growth, in a time which is suboptimal. E.g. snowdrop tricked into flowering early and got stuck in ice. Mismatches or asynchronies highlighted early on in IPCC reports. 1990s. Crucial importance in community function, interaction between plants, animals, soil organisms. Changes in climate can disrupt these synchronies. Big networks collect phenological data but volunteers. Not all species change at the same rate, leading the mismatch.

Mismatch concept: 1. Mismatch has negative fitness effects + 2. Best response is to track seasonal optima. If you characterise it a bit, the idea could be that before climate was changing, biological events by evolution were take place at optimal timings. Now if these seasonal optima and changing you would expect to see negative fitness effects and adaptive response would be to track the seasonal optima.

If you look at demographic consequences they are less studied than the shifts themselves. One paper, 400,000 phenological time series in one paper. 75% showed response to climate change. Not so much done on the actual consequences. We did a review and four 4 other studies that mentioned demographic consequences, and 62 mentioned something. Either effects on pop size/reproduction/survival. These show mixed responses. Advancing phenology’s would have no negative effect on survival/reproduction in some cases. Pop decline/growth in some cases. Unclear what’s going on!

Clarkia rubicunda – native plant in California. Bombus terrstris – bumble bee. Similarities in how they grow. Both annual. They have first growth phase, vegetative growth. Then switch, flower and start investing resources into reproduction. Bumble bee shows similar thing. First to grow colony with workers, more workers = more growth. Switches to produce sexuals. In this case males. The kind of model which was developed in the 70s to describe this is called the dynamic energy allocation models. Flowers would have vegetative part and reproductive part. The vegetative part increases your production. Measure in the end reproductive output. This results in vegetative growth phase then switching time then investing in reproduction. Similar model developed for bees. Optimal switching time = length of season – 1 / production. This means that when p is high you should wait to grow, closer to end of the season. Invest as long as you can, towards the end your switch.

We have extended this in various ways. Firstly, we have looked at seasonal variation in production rate (p not being constant). Size dependent relative growth rates, where productivity doesn’t increase linearly with size. E.g. because when you get bigger plant you start shading yourself, interfering with yourself. Intraspecific resource competition where the production depends on how many individuals are competing for that resource. Also, interspecific resource competition, multiple species competing for resource.

Seasonal variation in production rate. Example, bumble bees how in different environments, semi-natural, agricultural dominated, different distributions of seasonal resource. To get a different understanding of this we normalised the timescale from zero to one, extracted the shape function – the area under the curve is one – describe this as shape x total productivity. From there you arrive at a general graphic solution to this problem. This is your shape function. You can calculate the cumulative integral of that shape function. You can just plug in your productivity level here, then you invert that and you can kind of get your optimal flower term as functional productivity for any shape in the end. So this we can get the complete overview of how changes in seasonal productivity rates is affective optimal timing. For example, is this is the relative growth rate, then if you just increase the growth capacity, which is the total productivity, you will see that that always increases regardless of the shape. You can look at the different components of this shape function for some change in the resource peak level and we look at that one on its own you see that the optimum timing increases, late peak, late optimal timing. We looked at the spread for example, it depends on the productivity level. If you have low productivity and you increase the spread you should flower earlier. Whereas if you have high productivity and increase the spread you should flower later. That’s the main results.

We can then try to look at how if you change different components of this shape then, we can see what happens. If we at the same time change this total growth capacity and the productivity peak date, then actually in this case the optimum time shouldn’t change. It should advance because you have an earlier peak, but at the same time increased productivity should make you flower later. It’s possible that not changing is an adaptive response.

Size dependent relative growth rate. In some cases, you find exponential growth. At some point you would have some limitations setting in. Self-shading in plants, social insects – growth which levels off with size, possibly due to increased metabolic cost when larger, harder to get round the colony, more social unrest. If we have plants that do not have exponential growth, we see that increased productivity should reproduce earlier. This is because with limitations you don’t get so much back if you grow more. Might as well switch to reproduction. Internal growth constraints switch direction of optimal response to change.

Colony growth experiments. Working with colonies in lab in different conditions, different levels of nutrition/pesticides. When colony grows, consumption rate levels off. Indicates levelling off of production rates with colony weight. Should expect that if we increase productivity, amount of resources, you should switch to reproduction earlier – experiment showed this.

Effects of resource competition. When bee has emptied flower, it will be less food for others on that flower. Can expect if you have lots of bees foraging, the amount of forage will decrease. Resource per capita decreases. As workers get more numerous, resource per individual decreases. Interested in optimal switch point. If pop switches early there will be lots of resources left. If colony grow for long time, less resources left, will not be able to reproduce so much = more resources. System can be invaded by a strategy using an earlier time. Link together many years. Reproductive output gets fed into next year’s dynamics. Higher the sexual output in year one, more established year two = strong competition.

Max pop size you should reproduce earlier to reduce competition. ESS = evolutionary stable state. Somewhere in between. If you start thinking from this point, the pop reproducing early. Can be invaded by late reproducing strategies that use more resources. If you start here, reproduce v late, would grow so big they would deplete resources, making it advantageous for earlier strategy to come in. If season length increases, reproduce earlier to avoid competition, a bit earlier to reach ESS and later to increase pop max. Depending on how strong the resource comp is, you get dif responses. None of them are tracking resource perfectly, because if the trade-off between growth and reproduction. Need some time to grow and some time to reproduce. Also look at pop size. As resource peak date increases, pop size and timing of production increases.

We start at evolutionary equilibrium, pop growth, at some point grows slow due to increases comp, switches to reproducing sexuals. Later flowering peak, immediate response is more energy for sexuals, higher reproductive output. Leads to more colonies. Some evidence if you introduce red clover flowering late gives big boost in reproductive output. If you add adaptive response, use resources to increase colony growth rather than reproduction. Reproductive output goes down. Long term the system may be invaded by late reproducing species.

Effects of interspecific competition. More species competing. Niche diversification. Different species use different resources. Classic example, short and long tongue bees. Short corolla, long corolla. Also use different parts of the season. Depending on tongue length you can access different numbers of flowers at different times of the year. Different amount of resources available. Plug in the bumblebee model. Consider colony initiation (by queen who lays worker eggs) and switch to reproduction.

Consider how these strategies evolve in the resource landscape. Might expect not much point starting colony earlier but should evolve to use different resources. Finding the ESS using adaptive dynamics. Use adaptive dynamics to calculate evolutionary change.

Four plants flowering at different times. Simplest case everything shifts forward. What if you have a-symmetric shifts of resource, affecting species differently.

Adaptations to shifting seasons. Classic thinking is that you should just track another event. This could be some related event. Could be start of spring, snow melt, flowering time. What we see if that it might be perfectly adaptive to trail behind, or not change. Also see phenological responses in different directions. Plant and bee might shift in different directions. We could interpret it as a mismatch.

Demographic responses. Short term pop declines expected, but pop increases may occur due to competitive release.

Adaptive responses. Expected to restore population sizes (evolutionary rescue), but may cause pop declines (intensified competition).

Interspecific competition. Uneven shifts of seasonal resource distributions can cause asymmetric pop responses. Asymmetry reinforced by adaptation later. Phenological adaptation in one species may cause population declines in (or extinction of) another.

Adative phenological responses can be quite variable. Associated pop trends can also vary. Depends on life history trade-offs and competitive effects. Eco-evolutionary modelling can help us understand and analyse apparently idiosyncratic responses.

We have Ana and Richard, they are doing these kind of big colony experiments. Developing more detailed demographic model to capture dynamics within the colony because it’s when you know a lot about the system you realise it’s not so simple. Bees – one important thing is that the Queen lays egg and then that could take 20 days before that worker comes out. Might mean a lot of things when you think about how to adapt to seasonal shifts.

Seminar Four

The complex consequences of simple sociality in the wild

Josh Firth, Oxford University, Department of Zoology

5th December 2019

Seminar Five

Reconstructing the spread of bacterial mobile elements in space and time

Francois Balloux, Sillwood Park, Imperial College London

10th January 2020

Seminar Six

Managing fisheries to protect dependent predators

Simeon Hill

16th January 2020

Seminar Seven

Effects Temperature on Microbial Metabolic Rates: Linking Individual Responses to Ecosystem Impacts

Tom Smith, Imperial College London

23rd January 2020

Seminar Eight

The phylogenetic signature of interspecific competition in birds

Jonathan Drury, Durham University

30th January 2020

Seminar Nine

Sex, Drugs and Ecosystem Services: the paradox of plant toxins in nectar

Philip C Stevenson, University of Greenwich, Kew Botanical Gardens

6th February 2020

Seminar Ten

Conserving Genomic Diversity in a Changing World

Mike Bruford, Cardiff University

13th February 2020

Seminar Eleven

Evolutionary causes and consequences of avian dispersal syndromes: the importance of individual variation in colonisation processes

Marion Nicolaus, University of Groningen

27th February 2020