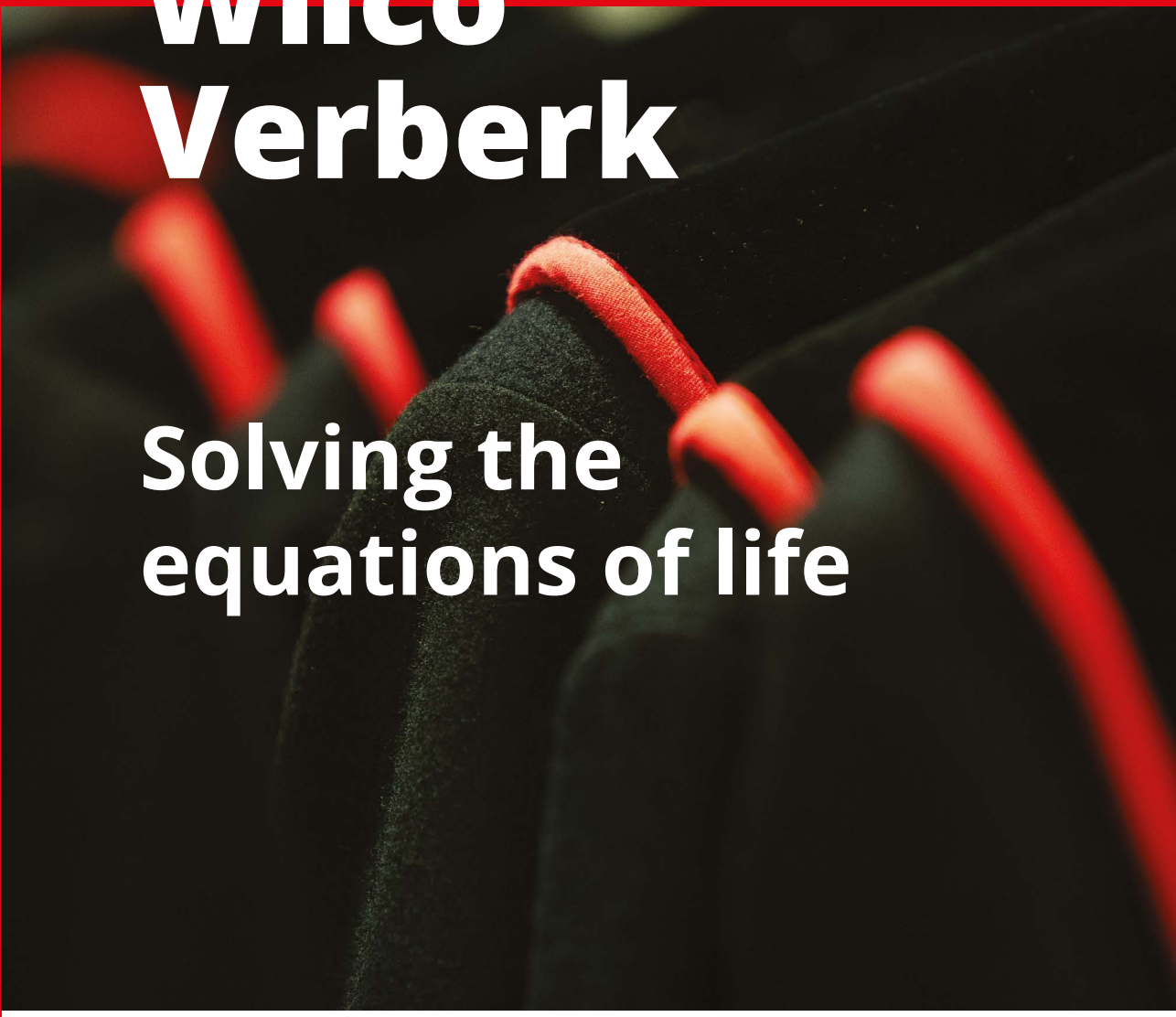
# Inaugural lecture

prof. dr.

# Wilco Verberk



## Solving the equations of life

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Wilco Verberk (1976, Oploo) is Professor of Functional Ecology at Radboud University. He studied biology in Nijmegen and then worked at Stichting Bargerveen on peat bog restoration. There, he completed his PhD alongside this regular work. As a postdoc, he worked in Plymouth (UK), before returning to Nijmegen as a lecturer. He investigates how temperature and oxygen shape life. Integrating ecology, physiology, and evolution, his work is widely recognized, as evidenced by major awards, including an NWO VIDI grant and the Dutch Zoology Prize. Next to these academic accomplishments, he holds a special position as father of Saar (2005), Toon (2007), Guus (2010) and Koos (2014).

Solving the equations of life takes the reader on a journey alongside three seemingly simple but fundamental protagonists of life: temperature, oxygen, and size. Each of these elements reveals a core principle of biology, from the near-exponential influence of temperature on the rate of living, to the pivotal role of oxygen in the evolution of complex life, and the continuous balancing act that shapes organismal body size. Insights from laboratory experiments are connected to patterns observed in nature and milestones in the evolution of life, such as the emergence of photosynthesis, the Cambrian explosion, and mass extinction events, are woven together with the aim of classifying species, themselves different answers to the “equations of life” into an ecological periodic table.

This book offers an inspiring blend of science, storytelling, and synthesis, aimed at both specialists and a broadly curious audience.

**SOLVING THE EQUATIONS OF LIFE**

# Solving the equations of life

*Inaugural lecture, delivered upon acceptance of the Chair in Functional Ecology at the Faculty of Science of the Radboud University, on Friday, February 6, 2026.*

by Prof. Dr. Wilco C.E.P. Verberk

**Solving the equations of life**

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## Introduction and learning objectives

I would like to start by welcoming you all to my lecture, or in this case, the written version of this lecture (for the recording itself, see the QR-code). I realise many of you do not go to the university on a day-to-day basis. Inaugural lectures tend to focus on research but at the university we also educate the next generation. So rather than telling you about the important work we do as educators, my idea here is to instead demonstrate this to you. So, the lecture will give you a flavour of what it is to be in university, listening to a lecturer, or reading the subsequent publication. I realise that there is a diversity in background knowledge so that the topics and concepts touched upon may be a bit tricky. That's okay. To understand the gist of the lecture, it is not necessary to be able to follow all of it. Like any good lecture we should start with the learning objectives. The first learning objective is to (further) improve your understanding of how science works. The Dutch title ('*Hoe het leven werkt*') lured you here and so we will at least cover some basic principles of life. This brings us to the second learning objective, which is to learn at least one new thing: Indeed, I would be disappointed if I couldn't manage to sneak a new fact into your knowledge base. In the lecture, I also stressed as a last learning objective that we should have a bit of fun along the way, as this will help solidify knowledge retention, but this is perhaps better conveyed in the lecture recording (see QR-code).

## A life in science

At the faculty of science, we biologists study many different species and ecosystems. For example, in my own research, I collaborated with colleagues to study the thermal biology of solar powered slugs, the distribution of freshwater fish, and effects of nature restoration on insects. Beyond biologists, many other excellent scientists work in our building. We have mathematicians who capture the world around us in pure algebra, physicists who take pictures of black holes, objects that swallow light. We have computer scientists who develop causal algorithms and chemists that develop hydrogels that mimick collagen fibers in our body for medicinal purposes. All of those fields you can arrange in various ways. Randall Munroe provided a nice example of arranging them along a single dimension of purity (Fig 1). In this cartoon, biology is considered to be a form of applied chemistry by the chemists, while chemistry in turn is considered a form of applied physics by the physicists. And then of course we have the mathematicians who are way above everybody else. Sadly, in our science faculty we do not have psychologists, so we as biologists are at the bottom of the food chain. Still, I can honestly say that I did marry out of my league by marrying Lies who is a mathematician. But more serious, this arrangement illustrates the breadth that I would

like to bridge in my lecture, going from biologists who study life and mathematicians who develop equations and all the fields in between. I believe all of these fields have ways of inspiring one another.

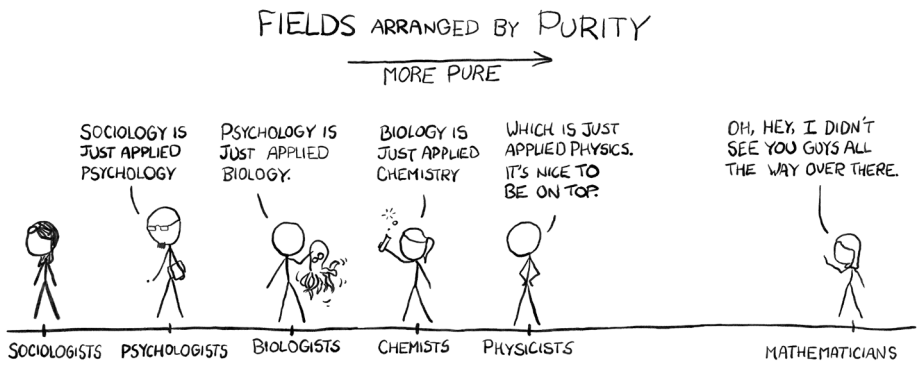


**Figure 1. Arrangement of various fields of inquiry along a single dimensional of purity. Image credit: xkcd.com.**

## Temperature

In this lecture, I will introduce three main protagonists or main characters. Each protagonist will also illustrate a key principle. The first protagonist is Temperature, illustrating the principle of useful approximations. If we consider temperature, we might have a clear notion of what it is. For example, the room temperature where we are now maybe around 20°. And physicists have equations that include temperature, such as the ideal gas law (eq 1). According to this equation, the volume multiplied by the pressure is a constant, but that constant is not really a constant, but in fact dependent on temperature (eq 2; with n being the number of moles, and R being the gas constant, equal to the product of the Boltzmann constant and the Avogadro constant). But actually, temperature is defined as the kinetic energy of individual molecules. So, the integrated effect of all those molecules moving around in the room can be transformed in a useful approximation by saying that the room temperature is around 20°C. Such a useful approximation illustrates that we don't need to have perfect knowledge in order to apply that knowledge. For example, we all have refrigerators at home, and they are based on the ideal gas law: They work just fine without having to measure the position and the speed of every gas molecule.

***Pressure×Volume=constant*** (eq1)

***constant=n ×R×Temperature*** (eq 2)



Although we humans often complain about the temperature (too warm, too cold), temperature is much more important for ectotherms, colloquially known as cold blooded animals. A fun fact of some relevance here is that over 99% of animal life is cold-blooded, regardless of whether you express this in terms of biomass, numbers of individuals or numbers of species. Temperature affects the rate of living in a near-exponential manner (Krogh, 1916; Clarke & Fraser, 2004). Therefore, as things heat up, the energy metabolism of ectotherms is sped up and it is sped up at increasingly faster rates. To deal with such nonlinearity, we turn to mathematics. One approach to deal with this nonlinearity, which I think is most intuitive, is the $Q_{10}$ approach. The $Q_{10}$ value expresses the factor by which biological rates increase when temperature increases by 10° C. Typically, studies report $Q_{10}$ value around 2, so rates double for a 10° C increase (i.e. 100% increase). Calculating the $Q_{10}$ value is quite straightforward (eq 3, with R1 and R2 being the biological rates at T1 and T2, respectively), especially when considering a 10° C temperature difference, but it can be (re)calculated for any temperature interval. To test your grasp of the concept, assume a $Q_{10}$ value of 2 and work out by how much rates would increase over a 5° C temperature interval (A: 33% | B: 50% | C: 41%). You can check your answer on the following page[1].

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{(10/(T_2-T_1))} \quad \text{(eq3)}$$

## Thermal physiology

So, if you grasp the concept fully, you will see that with warming, rates will eventually go through the roof and they cannot be sustained. This is indeed exactly what happens if you measure this in a real animal, i.e. a damselfly nymph (see Fig 2). Initially the rate of oxygen consumption, used as an approximation of energy metabolism (we'll cover this below), will follow an ever faster increase, reflecting higher demand for oxygen. However, eventually, limits to the capacity for extracting oxygen will set an upper limit to how fast oxygen can be taken up. Together with Hein van Kleef from Stichting Bargerveen, we measured oxygen consumption rates at a range of temperatures in various damselflies and dragonflies. We found evidence that some of the species that are in decline are also more susceptible to poor water oxygenation (van Kleef et al., 2025). Poor oxygenation results from the interplay between warming and in this case also reductions in acid rain, which means that the process of decomposition has accelerated which consumes oxygen in the moorland pools where these species occur. So, we can actually link information on thermal physiology from lab experiments to patterns on population trends derived from field data.

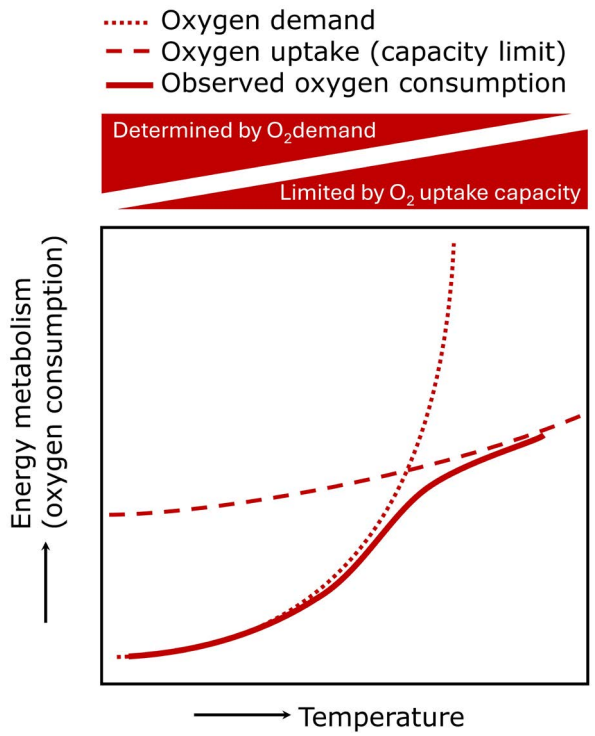


**Figure 2. Schematic illustration of temperature effect on observed oxygen uptake capacity. At low temperatures, demand for oxygen is also low, and oxygen consumption is governed by demand. As temperatures increase so does oxygen demand and hence oxygen consumption. However, at sufficiently high temperatures, the capacity for oxygen uptake will eventually become limiting, and the measured oxygen consumption will start reflecting uptake capacity.**

## The Periodic Table

Great, so we know how this works for at least these several damselfly and dragonfly species. But another fun fact is that there are over 10 million species on our planet. Typically, during an inaugural lecture, the new professor highlights a vision or a grand idea to solve a pressing matter in the field. Given the vast number of species, the pressing matter is if we can find shortcuts and extrapolate findings from one species to another species. One idea to think about this is to borrow a concept from another discipline, in this case the periodic table. And

[1] The correct answer is C: 41%. This corresponds to a multiplication factor of 1.41, or √2. Note that doubling the temperature interval from 5° C temperature to 10° C means multiplying with √2 twice, so you then get 2 again (√2 x √2 = 2). So, it the correct answer is C.



the idea would be to arrange species according to their biology into an ecological periodic table. To get an idea of how this would work, let's take a closer look at the periodic table (Fig 3). Most of you will remember this from high school: all the elements known to man are arranged in a two-dimensional table. So, we see that we already need one more dimension than we had when arranging the fields according to purity (Fig. 1). The arrangement of the elements in the periodic table is such that elements with similar properties are organised in columns. So, we can recognise noble gases in green and halogens in red. If we focus on a single row we see nitrogen, oxygen, fluor and neon lined up next to one another. Rows reflect increases in mass, but also differences in electron configuration, which has large consequences for the properties. To explain this simply, we can consider Neon to be perfectly content: it has exactly the number of electrons needed to fill all positions in its outer shell. It doesn't really want anything more, and like all other noble gases, it is reluctant to engage in chemical reactions. The situation is very different for Fluorine, which is so close—just one electron short of reaching the perfect configuration. In a sense, Fluorine is a Neon wannabe, with a strong appetite for that final electron. We make use of this reactivity every day: fluoride, the active component in toothpaste, helps kill pathogens. Oxygen is only one step further away. It is therefore also reactive, but less of a Neon wannabe than Fluorine. This has allowed oxygen to accumulate in our atmosphere and fundamentally transform how life works—making it well deserving of a paragraph of its own.

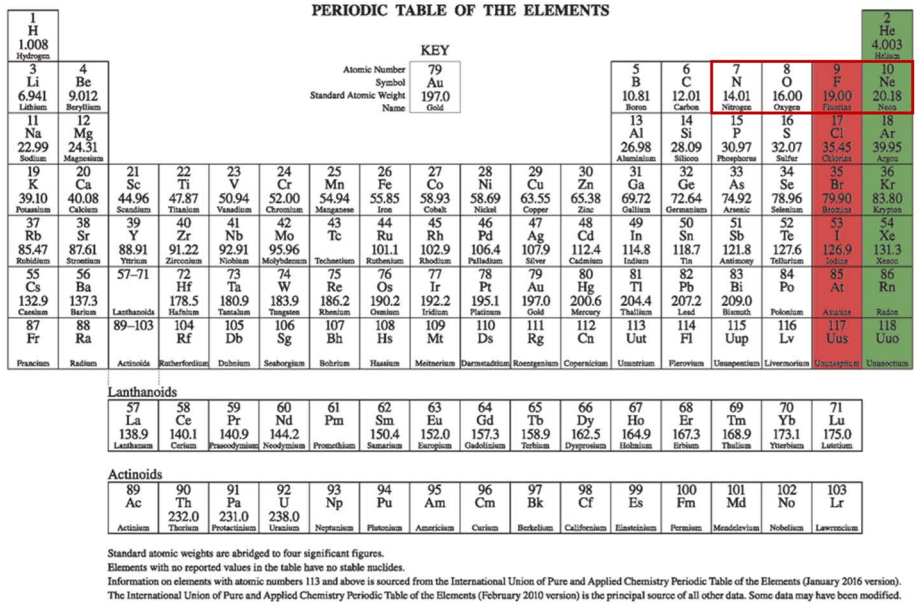


**Figure 3. Periodic table with halogens highlighted in red and noble gasses in green. The row with Nitrogen, Oxygen, Fluorine and Neon is also highlighted (see text for details).**

## Oxygen

So, the second of our three main protagonists is Oxygen. Oxygen is most familiar to us as the second most abundant gas in the atmosphere, making up approximately 21%. Each oxygen molecule consists of two oxygen atoms. Oxygen is so familiar to us because we are all addicted to it. Without oxygen we get severe withdrawal symptoms after about a minute and that is because we utterly depend on oxygen for liberating the energy stored in the food we eat. This is best exemplified by burning carbohydrates, composed of Carbon and Hydrogen atoms. Digesting food, or allowing the carbohydrates to react with oxygen, produces waste products like carbondioxide and water and generates the energy to fuel the fire of life[2].

Obviously, we tend to think of this process as a good thing, and this view is also reflected in popular fiction such as Star Wars. There, the Force is a living energy that permeates all life and makes everything possible. In the more recent movies, they do away with the mysticism of the earlier movies and explain that midiclorians are responsible for generating this life force. This is a clear analogy to the mitochondria in our own cells - the organelles where oxygen is being used to produce energy. So, there is a nice parallel from the midichlorians in Star Wars and our own mitochondria. Interestingly, the analogy also runs deeper: within our mitochondria, the energy that is released from food is used to shuttle protons across the inner membrane, which creates a proton motive force (Fig 4).

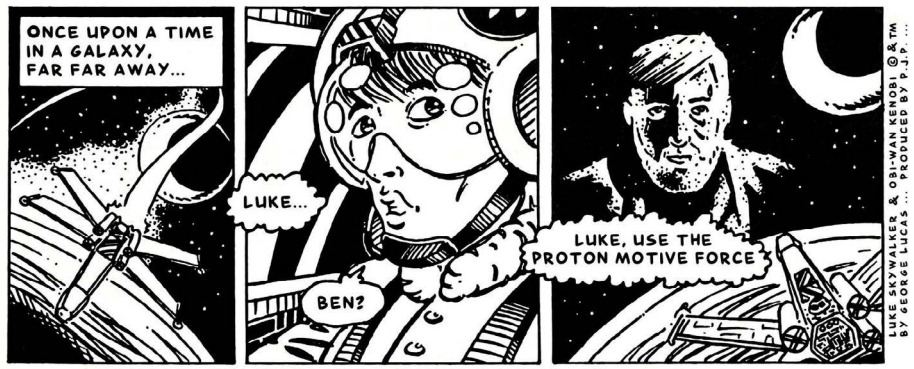


**Figure 4. The analogy between pop culture Star Wars and mitochondrial oxidative phosphorylation. Credit: Pierre van der Steen.**

[2] Note that burning, or oxidizing, lipids, carbohydrates or proteins takes different quantities of oxygen, but also generates different quantities of energy, so that for all food types, the net result is that per mole of oxygen about 440 KJ is being liberated. Because of this constancy across food types, scientists often measure oxygen as a proxy for energy metabolism.



Now, I don't want to spoil too much about Star Wars, but Anakin is actually Darth Vader - sorry. The reason I bring this up is that, like Anakin, Oxygen also has a dark side. Sometimes oxygen only gets a single electron, turning it into a Neon wannabe like Fluorine, aggressively reacting with the first molecule it encounters. This “dark side” of oxygen, the creation of reactive oxygen species, contributes to ageing and, ultimately, death. So, oxygen is linked to key events in life (Box 1), including its end. While this may not sound like a fun fact, it is highly functional (much like the title of my chair). Each protagonist illustrates a key principle, in this case that life is a balancing act. Because of the two-faced nature of oxygen, it must be delivered to the mitochondria in just the right amount: too little limits energy production, while too much increases damaging reactivity. That is of course why we have hemoglobin, why we have blood cells, why we have a heart and a circulation system that adjusts dynamically to our demand for oxygen. If oxygen was only good, then we would just flood the cells with oxygen. But it is not, and we don’t.

### BOX 1 Oxygen has shaped key events in life

We humans are very used to having plenty of oxygen around, about 21% as mentioned. But this was not always the case. One of the really remarkable things about science is that we can actually reconstruct how much oxygen there was in the atmosphere far back in time (Berner et al., 2006; Chen et al., 2022).

So, if we look at this kind of record, we can place ourselves in the present day and then go all the way back to the beginning of the planet—about four billion years ago. And for a very long time, not much seems to happen. Then, eventually, oxygen appears (Fig 5A). But that is not the whole story. The reason is that most of the interesting changes are compressed into the lower part of the graph and are easy to miss. So let me take a small leap and show you exactly the same data in a slightly different way (Fig 5B). The only thing that changes is the y-axis: instead of a linear scale, we now use a $\log_{10}$ scale. The difference is important. In the first graph, changes are additive; in the second, each step represents a tenfold increase. And suddenly, you can see that a lot is happening below 1% oxygen—things that were essentially invisible before.

Now, we can start to pick out some key events. Around 2500 Mya ago, for example, is the onset of photosynthesis. At this point, certain bacteria evolved the ability to split water ($H_2O$) and use some of it for photosynthesis. The oxygen in our atmosphere is, in fact, a waste product of this process. Oxygen levels rise a little—but not dramatically, because much of it is immediately consumed again in other reactions. Remember that oxygen is quite reactive (though not so much as Fluorine), and so it can only begin to accumulate in the atmosphere, after having oxidised other substances such as reduced minerals (mostly ferrous iron), hydrogen sulfide and organic matter.

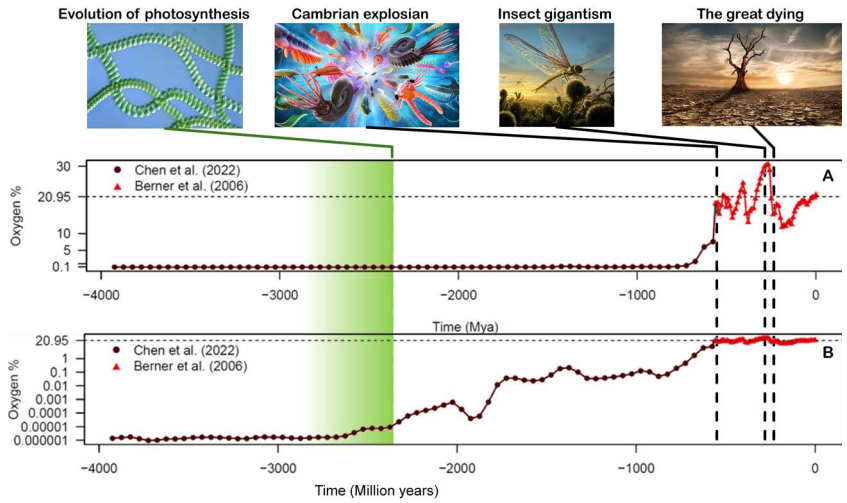


**Figure 5. Key events related to oxygen during the geological history of our planet. Note that panel A and B show the same data, but in panel B they are plotted on a $\log_{10}$ scale.**

Further along, around 540 Mya ago, we encounter the Cambrian explosion. Basically, all of the eukarotic life that that we know and cherish today has actually started from the Cambrian explosion. And, give or take a few hundred million years, this coincides quite nicely with a rise in oxygen levels. We also see giant insects that capture the imagination at 300 Mya ago: Griffenflies, or protodonata—with wingspans of up to 70 centimeters. These existed during periods of particularly high oxygen levels, when vast coal-forming forests locked away large amounts of carbon, allowing oxygen levels to soar. And then, on a less cheerful note, when oxygen levels drop sharply, we see mass extinction events. The biggest and worst so far, known as the Great Dying, took place 252 Mya ago, during which around 90% of marine life and 70% of terrestrial life were wiped out.

So, fun fact—or perhaps not such a fun fact—oxygen, when viewed over very long timescales, is closely tied to some of the most important events in the history of life.



## Size

Size is the third protagonist. I think it's great to be large (or at least tall). With my length of 1.98 meters, I might be a bit prejudiced, but there are distinct advantages to being large. For example, aquatic foodwebs are strongly size structured: If you're the biggest fish, you're less likely to be eaten. *Within* a given species, we observe that the largest individuals also tend to produce the most babies. They also tend to be better in competitions. However, if you look at how size is distributed *across* species, the majority of species are small. For example, if you take the mean size of the smallest and the largest bird species, most birds will be smaller than this mean size. The same applies if you take mammals, insects, or any other animal group: we always see that the majority of species are smaller than the mean for that group. Obviously, being large is not without disadvantages. But what would these disadvantages be? Again, I have three possible answers, and you can test your knowledge (A: Growth takes time | B: Growth takes resources | C: It's lonely at the top). You can check your answer on the following page[3].

Given that size has both advantages and disadvantages, size is also a balancing act. With so many factors involved in this evolutory tug of war, body size is such a great integrator. This explains why size is so popular to study in biology. It reflects the evolutionary outcome, giving information on what the species was selected to do. If they grow quickly to a small size, then they probably die quickly and have successfully faced (and adapted to) a very different set of environmental challenges than a species that grows more slowly to a large size.

I should point out here that it's not just the size of the whole body that gives important clues to the life-history of an animal, but also the cells that make up the body (Verberk & Czarnoleski, 2025). Again, we have this balancing act (Szarski, 1983): Animals with large cells tend to be very much geared towards energy conservation. You can think of this as the energy A+++ label. In contrast, animals composed of small cells tend to have a much more wasteful energy life cycle, but this enables them to take up more resources in a shorter time, giving them greater physiological power (provided resources are not limited). Thus, from the perspective of the cell-size-balancing-act, rapid growth rate and high energetic costs tend to be linked and this pattern has indeed been described across a wide range of species in the literature (Kooijman, 2013). Major evolutionary transitions across the tree of life can be traced back to changes in cell size, revealing cell size to be fundamental to the ecology and evolution of life (Verberk & Czarnoleski, 2025).

## *Ceteris paribus* (All else being equal)

Having already treated the effect of temperature on the rate of oxygen consumption or metabolism, we can now do the same for mass. The null hypothesis here would be that the larger the animal is, the more oxygen it will require, '*ceteris paribus*'. '*Ceteris paribus*' is Latin meaning so much as 'all else being equal': Provided none of the rules change, we would expect an animal that grows to double its mass to also have double the rate of energy metabolism. Again, we turn to log-log plots (see box 1) and we can test the null hypothesis by investigating the scaling exponent of the resultant power law. According to this null hypothesis, proportional increases in both mass and metabolism would yield an exponent of exactly 1, conforming to isometric scaling. However, this is not what actual data on mass scaling of metabolism show (Fig 6).

For both endotherms, i.e. warm-blooded animals (depicted in red, and remember, these make up less than 1% of all animal life) and ectotherms or cold-blooded animals (depicted in blue, the vast majority), the scaling exponent is less than one. This means that metabolic rate increases with body mass, but less than proportionally. As an aside, the data in this graph represents years of work undertaken by many different scientists around the world, and which were subsequently collated by Craig White and colleagues (White et al., 2019).

What's even more interesting is that we can analyse the data in a different way and show that these scaling exponents are not the same for both groups (P<0.001; see Verberk et al., 2020 for details on the analysis). The P-value here is a popular way among scientists to indicate the statistical likelihood of finding a difference purely by chance. In this case, the chance that the difference between both groups is just random noise is less than 1 in a 1000. Thus, if you - like many if not most scientists - believe in P-values (but see Halsey et al., 2015 for an in-depth discussion), it is highly likely that there are fundamental differences in mass scaling of metabolism between endotherms and ectotherms. This has been pointed out before and will likely need to be pointed out again, because scientists can be notoriously stubborn. If you're encountering this idea for the first time, you might think: "Okay, no big deal." But in some research settings, the idea of a single, canonical scaling exponent is treated almost like gospel—and questioning it is like bringing up privacy concerns in a meeting with Apple or Microsoft.

So how much does it matter if the scaling exponent is 1 or 0.8 or whatever value? One way to illustrate this is to express the energy use in Joules per day per gram. If we standardise accordingly, we humans use about 100 Joules per day per gram. But, what about my favourite

[3] The correct answer is: all of them: A: Growth indeed takes time, during which mortality risks accumulate. Since dead animals tend to not reproduce, it doesn't always pay off to try and be the largest. B: It is also true that growth takes resources, which requires animals to risk going out for foraging, exposing themselves to dangers. C: Again true: as you go up from the base of the food chain, there is energy lost, approximately 90% for each level (primary producers > consumers > secondary consumers > … > top predators). So, at the top, there is very little energy left to build large populations, making them more prone to extinction.



beetle, *Colymbetes paykulli* Erichson, 1837, which weighs less than 1 gram? Amazingly, this beetle also uses approximately 100 Joules per day per gram. Being heavier means we tend to use less oxygen, but since we are warm blooded, we use more oxygen and the two balance each other out. Indeed, when you draw a scaling relationship with an exponent of 1, we are both on the same line.

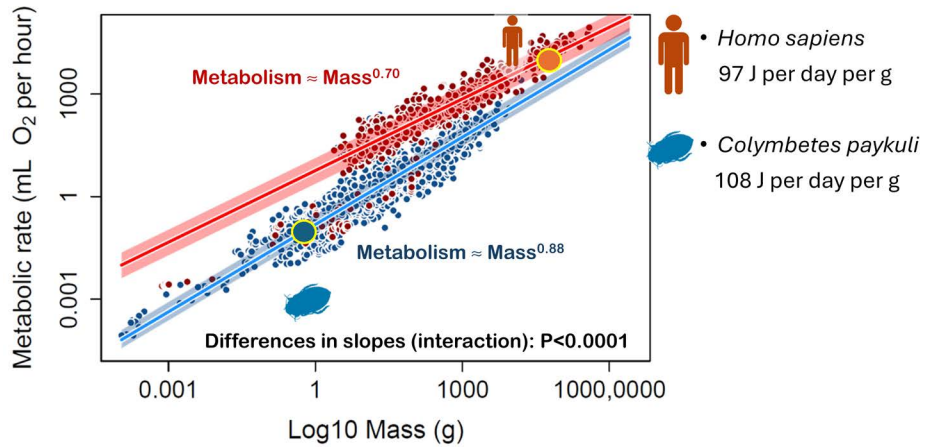


**Figure 6. Allometric mass scaling of energy metabolism (i.e. a power relationship with an exponent smaller than 1). Endotherms (mammals, birds) are shown in red, with *Homo sapiens* L. 1758 as an example. Ectotherms (the other >99% of all animal life) are shown in blue, with *Colymbetes paykulli* Erichson, 1837 *as an* example. Note that axes are $\log_{10}$ transformed.**

Since we are having so much fun with log-log plots, we can take this a step further. The cool thing is that we can extrapolate orders of magnitude and plot the sun on a similar graph (Fig 7). Whether this indicates some cosmic regularity in energy scaling or whether this is purely coincidental I do not know (but if you are an astronomer, feel free to plot for yourself energy output against mass for different types of stars). You will remember that the scaling exponent for this relationship was less than one. So, accordingly, if we use the same standardization as above and calculate the energy of the sun on a per gram basis, it's only 0.016 Joules per gram per day. So, the fun fact here is that each of us will burn about 6,000 times more brightly than the sun on a per gram basis. A slightly more serious consideration here is that we should be mindful about how we make comparisons. Is the correct way to just express energy metabolism on a per gram basis to prevent comparing apples and pears? We have seen here that this actually introduces bias and if we know the scaling relationship, we can use that to make comparisons controlling for – in this case – known effects of mass, enabling us to keep all else equal ('*ceteris paribus*').

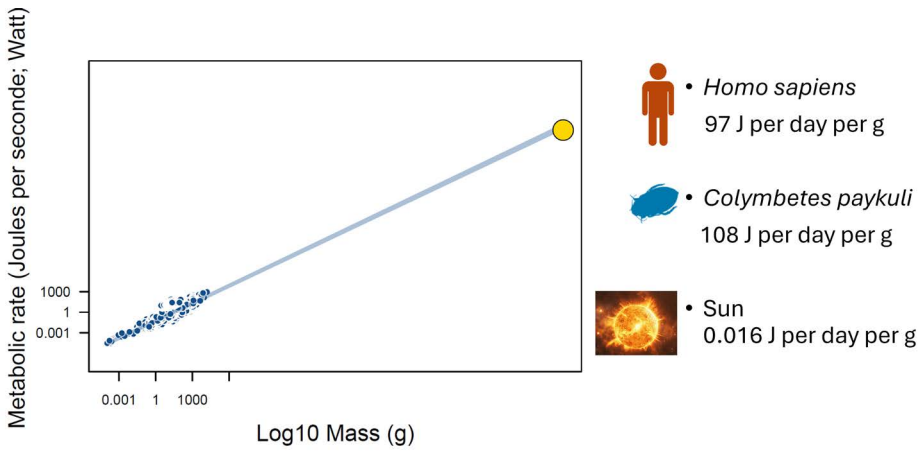


**Figure 7. Extrapolating the mass scaling of energy metabolism for ectotherms from figure 6 across orders of magnitude (and converting the units from oxygen consumption to Joules), allows the sun to be plotted in the same graph (yellow).**

## Size, temperature and oxygen

To bring together the three protagonists of our story, let's consider the following evolutionary puzzle that combines body size and temperature. Recall that body size is a powerful integrator, and that to grow large one needs time and resources. At higher temperatures, organisms tend to grow faster—a pattern that fits a broader theme, as we also saw increased energy demands in warmer conditions (Fig. 8). If faster growth in warmer conditions does not surprise you, you may be puzzled to read that most ectotherms actually reach maturity—or stop growing altogether—at a smaller size (Atkinson & Sibly, 1997; Hoefnagel et al., 1018). In other words, they grow faster but the rate at which they mature is sped up even more (note that if both growth and development had the same $Q_{10}$, size would be invariant to temperature). So, their entire lifecycle is super charged. This empirical pattern is called the Temperature-Size Rule (Fig 8), and even after writing an extensive review about the topic (see Verberk et al., 2021), I find this a mind-boggling pattern. To see why and illustrate the complexity, let's first consider the null hypothesis. If we start from observed faster growth, we would expect, *ceteris paribus*, maturation at a larger size in warmer conditions. And this is exactly what we find if we change the amount of food during development: high food treatments result in faster juvenile growth and larger adults. So clearly not all else is equal.

Given the information above, you could come up with the following explanation, taking the observed smaller size at maturity as a starting point: Larger animals need more oxygen, but at higher temperatures, animals also need more oxygen and so they run out of oxygen



sooner/at a smaller size. This explanation has indeed been put forward in the literature (Pauly, 2010)[4], but it is wrong or at least incomplete. To see why, we can plot growth (i.e. the derivative of the size-time relationship), which makes it clear that the effect of warming is different depending on size: Warming initially increases growth rate in small individuals, before reducing it in large individuals. This means that we cannot treat this problem as set of independent, linear equations. Instead, there is a three-way interaction between time, size and temperature. Oxygen can be a possible resolution to the temperature-size rule, but for this mechanism to work, taking up sufficient oxygen should also be challenging in a size and temperature dependent manner, being much more of a problem for large animals and for animals in warm conditions.

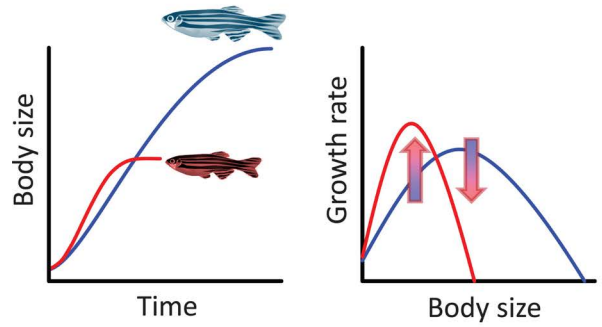


**Figure 8. Schematic illustration of the temperature-size rule. Temperature alters growth trajectories such that animals (such as zebrafish) in warmer conditions reach maturity at a smaller size compared to those in cooler conditions (left panel). The effect of temperature on growth (the derivative of size over time) changes through ontogeny in a temperature dependent manner (right panel). Initially at small sizes, warmer temperatures stimulate growth, but as animals grow further, warmer temperatures start to reduce growth. Note that zebrafish do not change color as a function of rearing temperature: red simply illustrates warmer conditions and blue illustrates colder conditions.**

Postulating a mechanism whereby oxygen deficiency is size and temperature dependent is one thing, but as scientists, we want to proceed to the next level which is to perform a test with independent data to see if this idea can be supported or refuted. As we already saw,

[4] I was in doubt if I should cite the reference, partly because summarizing ideas laid out across a whole book in a single sentence is bound to be incomplete, opening myself up to my own criticism. But I believe the book makes for an interesting read. Yes, I do not agree with what it says about the temperature-size rule, but my intention with adding the reference is not naming and blaming. Indeed, all models are wrong, but some are useful. It illustrates a way in which science works: The scientific process is one of debate, ideas, incremental improvement, sometimes exploring a direction that turns out to be wrong. But visionary ideas, hypotheses and generalisations, even if they turn out to be false or incomplete are highly important, stimulating debate on the underlying assumptions, exquisite experiments to test these underlying assumptions and vast data compilations to test if generalisations hold. As such they should be credited and citations are an important currency in science (for better or worse).

there is a strong interest in collating data from the literature on rates of oxygen consumption and thanks to such efforts we have been able to synthesise patterns across many different fish species (Rubalcaba, et al. 2020). Having all the data, we analysed them to test if patterns in oxygen consumption are consistent with the temperature-size responses mentioned before. For this we turn to mathematics and physics to supply us with the correct tools to solve the equations of life. We came up with two equations[5], which are shown below: one for oxygen demand and the other for oxygen supply (see Figure 2).

$$O_2 \text{ demand} = \delta b_0 M^b e^{\frac{-E}{kT}} \frac{\rho O_{2,gill}{}^H}{\rho O_{2,gill}{}^H + K_m{}^H} \text{ (eq4)}$$

$$O_2\ supply = -A \times h_m\left(\rho O_{2,gill} - \rho O_{2,water}\right) \text{ (eq5)}$$

Without going into too much detail here (but please read Rubalcaba et al., 2020), we can easily recognise all the protagonists in these equations (**M**ass, **T**emperature and $O_2$, highlighted in red). The key innovation was that we combined both equations such that supply should equal demand. So we assumed that these two rates should be balanced, which is not a wild assumption given that animals cannot use oxygen at a higher rate than they can extract it (because this would generate negative oxygen values in the animal), nor can they use less than they extract (because the animal would then load up with oxygen and eventually explode). Combining the two equations yielded predictions that very well matched the empirical data. Both the model and the empirical data show that metabolism increases with increasing body mass and temperature (see figures 2 and 6), but the ability to take up more oxygen in warmer water becomes proportionally smaller in larger animals.

So, these independent data actually provide evidence for the notion that larger fish are more likely to run out of oxygen at these warmer temperatures. And we found this effect to be even more pronounced in actively swimming fish. So, if fish have to exercise (e.g. catch prey or escape predators), they will run out of oxygen sooner, especially if they are also large and swimming in warm water. Without laboring the point, we saw similar patterns again when using another set of independent data, this time on hypoxia tolerance (see Verberk et al., 2022).

## Solving the equations of life

A brief recap: We can work with useful approximations. We know that life is a balancing act, and that meaningful comparisons require us to keep things on a comparable basis (*ceteris paribus*). We also know that animals tend to grow larger in the cold, and especially when oxygen is abundant. And the opposite occurs in warmer, low-oxygen environments. But

[5] A colleague once told me that for every equation shown, you lose half your public. So, I am aware that by now, 5 equations later, I may have lost 96.9% (1-(1/2)$^5$ x 100%) of my readers. Still, I think math is important as it forces one to make the assumptions underlying any reasoning explicit. Thus, we need to embrace maths (and mathematicians), and I congratulate you, the reader, for your tenacity and perseverance.



these are not isolated effects, there are multiple balancing acts at play. We have already seen the balance involved in provisioning oxygen to mitochondria in precise amounts. Furthermore, effects of temperature and oxygen on cell size mirror those for body size, suggesting that there is a very similar balancing act for cell size as the one described in detail for body size (Leiva et al., 2023). Balancing acts are therefore at the heart of biology, and each can be described by a set of equations. Because there is no single solution to any of these balances, life can be seen as a collection of possible solutions. Species themselves then guide us, providing insight into how we can solve the equations of life: each one represents a particular way of resolving the balancing acts. By bringing these solutions together, we can begin to assemble an ecological periodic table.

## Towards an Ecological Periodic Table

We already saw that there are over 10 million species. Unlike some researchers who focus on one or a few model organisms, I have worked on quite a few different species over the last 25 years, ranging from cannibalistic crickets (Vogels et al., 2024), a historical reconstruction of the collapse of salmon stocks (Lenders et al., 2016), to heat tolerance in solar-powered slugs (Laetz et al., 2024). But a scientific study of all life would take much more than one lifetime. Assume we would be so arrogant as to say that only 5 scientific papers would be sufficient; that this would be enough to know about a species. To put this in perspective, a PhD thesis typically has that number of chapters. To put this number in another perspective, already approximately 200,000 papers have been published on just 4 species: *Danio rerio, Drosophila melanogaster, Daphnia magna* and *Caenorhabditis elegans* (7 of which I have contributed to). Thus even 5 papers a species would amount to a total of 50 x $10^6$ papers! This is approximately the same number of years (Yes, some researchers publish more frequently, but if we count all the hours of support staff and divide by the number of co-authors, I believe that one year for one paper is reasonable), which takes us back almost as far as the age of the dinosaurs! And if we would want to do a more decent job than just 5 papers, one could easily end up spending the same time studying all the species as it took them to evolve since the Cambrian explosion.

So that is a lot of work and frankly we don't have the time as biodiversity is in decline. But it is not just biodiversity declining. Oxygen levels in the atmosphere are also in decline (Fig 9). This figure illustrates a trick sometimes used by scientists, which is that the graph doesn't start at zero. Because of this, the decline appears to be quite large. Although the situation is not as dire that we are all gasping for breath, it is disconcerting that we can see a measurable decline, especially since this is within a timescale of just a few decades. Some back of the envelope calculations would estimate this rapidity of decline to be on an equal footing of the plummeting of the oxygen levels during the great dying. This is because we're burning up all the carbon locked away long ago, and this consumes oxygen. Not all the oxygen, and not yet, but it does illustrate that time is a limiting, non-renewal resource.

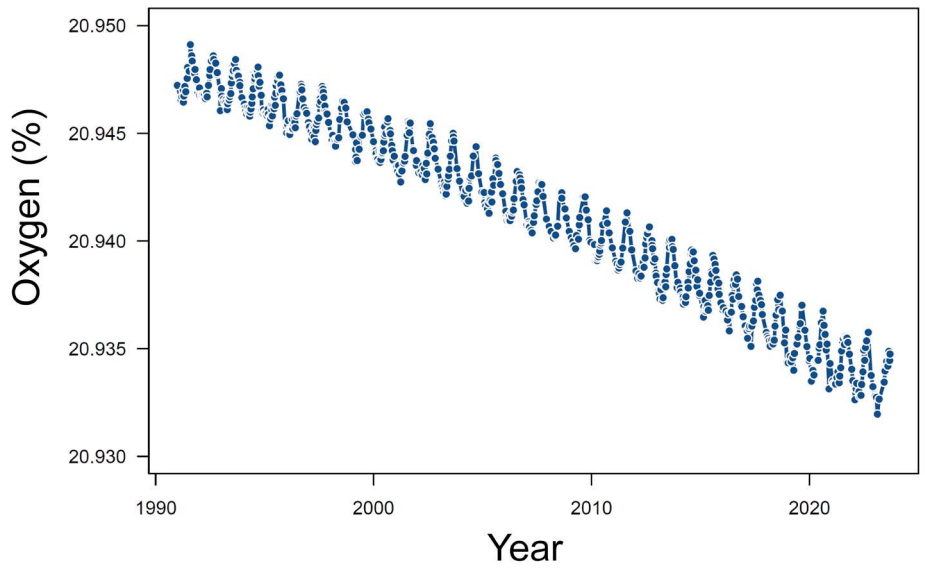


**Figure 9. Trends in atmospheric oxygen levels over the last couple of decades. Note that the axis does not start at zero. Yearly fluctuations represent seasonal fluctuations (similar fluctuations can be seen in atmospheric carbondioxide levels). Data source: Scripps $O_2$ Program (oxygenlevels.org).**

Are there solutions to obtain knowledge on the ecological periodic table without taking as long as going all the way back to the Cambrian explosion? One shortcut here is that in order to fit the equations of life, we do not need full knowledge. We have already illustrated this principle above, and if we have a couple of data points, we can fit a curve. If we know the relationship is linear, we could get away with having only two data points (in principle, but if you want to publish this, I advise against suggesting me as a reviewer). In fact, we could get away with even just a single datapoint, provided we know the line goes through the origin. What is important here is that we have a theory in place to inform us about the equation describing the relationship. But provided we have such equations, fitting a curve through some representative points is a possible shortcut.

A second solution is that we join forces and work together. We need all kinds of biologists, from theoretical ecologists and naturalists to experimental physiologists. And we need to share data so that we can genuinely expand our knowledge base. Together with several colleagues we started the ShareTrait initiative (Leiva et al., 2025), where we bring together information on key traits of animals. The way I usually explain this to other people is that we are trying to build a database without a preconceived question in mind. This is very different from how scientists normally approach things, where they have a specific question



in mind and then extract the data that is pertinent to answering said question. However, with this approach, another scientist with a similar, but slightly different question may end up extracting slightly different data from the same publications. By extracting data without a preconceived question, we hope to prevent duplication of efforts and create a common resource for all scientists.

So those are my two solutions to solving the equations of life for 10 million species that will help create an ecological periodic table.

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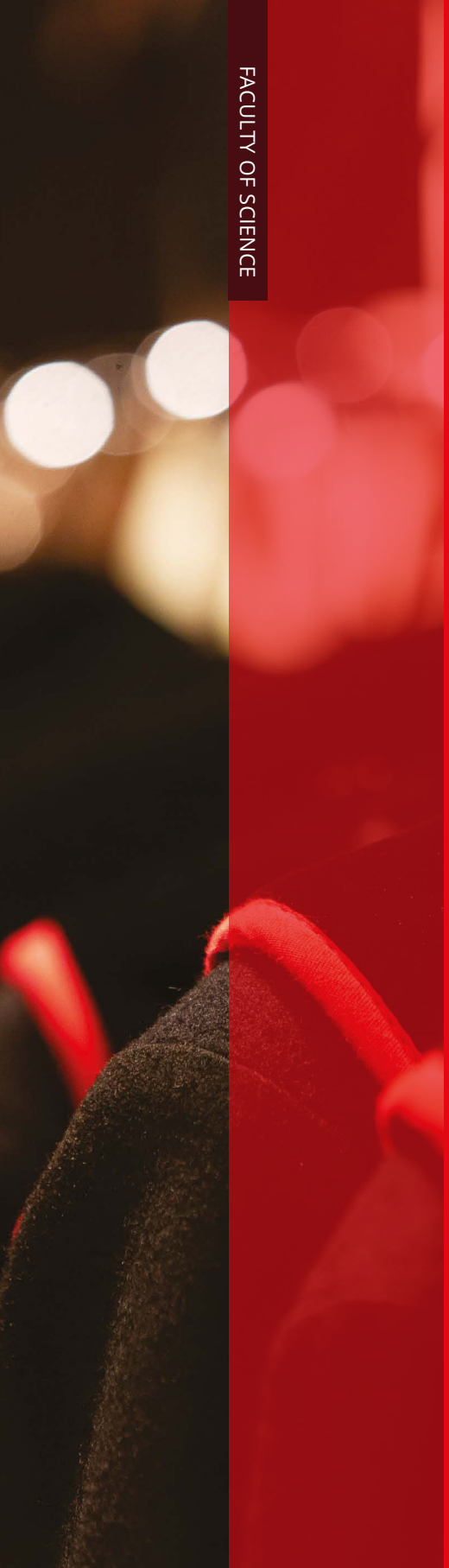

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