

Bioengineering the Biosphere?

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ABSTRACT

Our planet is experiencing an accelerated process of change associated to a variety of anthropogenic-related processes. Climate change and biodiversity decline are two facets of this phenomenon. The future of this transformation is uncertain, but there is general agreement about its negative unfolding that might threaten our own survival. Furthermore, the pace of the expected changes is likely to be abrupt: catastrophic shifts might be the most likely outcome of this ongoing, apparently slow process. Although different strategies for geo-engineering the planet have been advanced, none seem likely to safely revert the large-scale problems associated to carbon dioxide accumulation or ecosystem degradation. An alternative possibility considered here is inspired in the rapidly growing potential for engineering living systems. It would involve designing synthetic organisms capable of reproducing and expanding to large geographic scales with the goal of achieving a long-term or a transient restoration of ecosystem-level homeostasis. Such a regional or even planetary-scale engineering would have to deal with the complexity of our biosphere. It will require not only a proper design of organisms but also understanding their place within ecological networks and their evolvability. This is a likely future scenario that will require integration of ideas coming from currently weakly connected domains, including synthetic biology, ecological and genome engineering, evolutionary theory, climate science, biogeography and invasion ecology, among others.

Introduction

In a few human generations, our planet is likely to experience large-scale changes that will jeopardise the stability of our complex social and economic structures. Energy and demographic crises, biodiversity declines, increasingly frequent extreme events, along with water shortage and crop failure associated to climate change are already sending us warning signals (Scheffer et al 2001, Scheffer and Carpenter 2003, Scheffer 2009, Dawson et al 2011, Lenton 2011, Barnovsky et al 2012). We live in a time where the knowledge of our planet is greater than ever and the potential threads seem rather well defined. Scientists have depicted a grim perspective of our future. We are a major transforming force that is rapidly pushing our planet towards new, undesirable states. A consensus has emerged from climate science about a future, hotter planet that will make life difficult, if not simply incompatible, with a sustainable society (Lenton 2008). We have enjoyed a favourable window of 10.000 years, the so called Holocene period, where humans have been able to flourish as a dominant, creative and rapidly expanding species but also as a global geological force. The new human-driven era that emerges from the Industrial Revolution, the so called Anthropocene, is dominated by an increasingly obvious impact of human activities that are pushing the Earth outside its regulatory capacity (Steffen et al 2011).

As it occurs with many other complex systems (May 1977) continuous changes in parameters that control the state of given system often end up in catastrophic shifts once tipping points are reached (Scheffer 2009, Solé 2011, Hughes et al 2012). This is the case of the average concentration of carbon dioxide: once some critical levels are reached, our current climate state will be replaced by another global pattern resulting from a runaway greenhouse effect (Solomon et al 2007, New et al 2011). A macroecological analysis of energy use and economic activity also indicates that the current tendency might end in a social and economic collapse (Rockstrom et al 2009). Similarly, many ecological systems will face rapid declines towards degraded and even bare systems with no species left (Suding et al 2004). This is illustrated by arid and semiarid ecosystems (Rietkerk and van de Koppel 1997, Scanlon et al 2007, Kéfi et al 2007, Solé 2007) where warming, steady declines in rainfall and increasing grazing will trigger rapid changes towards a desert state and are specially vulnerable (Thornton et al 2011). Evidence for such sudden changes exist, as shown by the shift from a green Sahara to the current desert state, which took place 5500 years ago (Foley et al 2003). Rainforest ecosystems, reefs and boreal forests might also face serious declines (Barnovsky et al 2012, Hughes et al 2013). In some cases, as illustrated by the collapse of fisheries, they have already occurred while the awareness and reactivity of society to such sudden loss has been far from optimal (Scheffer et al 2013).

Although many studies have addressed possible ways for remediating these potentially catastrophic situations, the scale of the problem, the staggering economic costs and its accelerating pace constitute a major barrier to restore previous states in a sustainable way (Folke et al 2011). Moreover, we need to face the nature of our biosphere as a complex adaptive system with multiple interacting species, nonlinear responses, complex feedbacks and self-organizing patterns (Levin 2002, Solé and Levin 2002). In this paper I suggest a rather different approach, which requires an engineering perspective, grounded in the design of modified life forms and intervention. But, above all, requires a new merging of disciplines, particularly at the unexplored boundaries between synthetic biology and ecological theory. Because it requires humans as agents for Earth's transformation, the remediation strategies suggested here imply a modification of natural ecosystems. The advantages and drawbacks of this approximation, along with implementation strategies, are outlined below.

Terraforming Earth?

Restoring a sustainable Earth's state necessarily requires to confront the scales of space, time and energy on the planetary level. That means that whatever the solutions found, they go beyond any human standard engineering scale. Before looking at our own biosphere, let us first make a turn by considering the other single scenario where such engineering problem has been proposed, namely the problem of "Terraforming" Mars (McKay et al 1991). The idea is, in a nutshell, introducing artificial modifications triggering a runaway process capable of displacing the state's planet towards a new steady state where higher temperatures, water levels and thicker atmosphere would be present. That could be achieved through the use of greenhouse gases (Lovelock 1988) although at very high costs. It would be also achievable or by means of appropriate microorganisms (Rothschild and Mancinelli 2001) capable of adapting and growing under extreme conditions. In both cases, a relatively small perturbation is expected to get amplified, ultimately affecting the planet's geochemical cycles. The first possibility is unlikely to be feasible due to the associated costs. But the use of extremophiles, such as some bacterial species of *Carnobacterium* (Rothschild and Mancinelli 2001, Nicholson et al 2012) have been shown to tolerate extreme conditions (including low pressures and temperatures along with anoxia).

In this paper we will use the previous scenario as a starting point to discuss how the release of genetically manipulated organisms could be used to restore habitat and climate unbalances at local, regional and even global scales. Such possibility has not been raised before. Instead, within the context of global warming, existing proposals consider geoengineering (Lovelock and Rapley 2007, Schneider 2008, Vaughan and Lenton 2011, Caldeira et al 2013). In contrast with reduction of emissions, this climate engineering scheme (directed to mitigate global warming) operates directly on diverse physical or chemical factors. The cost of most proposed solutions is typically enormous, as a consequence of the massive scales involved. These solutions include a broad variety of possibilities, from hundreds of thousands of towers to capture carbon dioxide to trillions of small, free-flying spacecrafts. Lower costs but high risks are expected from using aerosols, to be injected in the stratosphere to counterbalance greenhouse gases (Lovelock 2008). Other strategies, such as iron seeding to trigger plankton blooms have failed to met their expectations. Even despite the limitations of these proposals, a common message is that the price of not preparing for the future will be much higher than the investment in any of the previous possibilities (Schneider and Mesirov 1976).

How to deal with the large scale problem that we face here? If geoengineering is not the right approach, what can be the alternative? We should look for feasible solutions capable of (a) solving the scale problem at a reasonable cost, (b) restoring the desired system's state over an appropriate time scale and (c) minimize the risks of undesired evolutionary dynamics. The approach suggested here is that such solutions might soon exist at the crossroads between ecosystem engineering (Odum and Odum 2003) and different approaches oriented towards engineering living systems, particularly synthetic biology (Drubin et al 2007) and genetic engineering of plants (Mittler and Blumwald 2010). So far, all these approaches have been developed within a lab or farm context where containment is a major concern (Church 2005, Dana et al 2012). Not surprisingly, biosafety issues related to the potential release of engineered organisms or genetic material have become part of the research agenda. Given all the unknowns, containment has been at the centre of these disciplines as much as their design principles. What I want to suggest here is precisely a rather orthogonal, but may be complementary: "Terraforming Earth" by engineering new synthetic organisms capable of counterbalancing undesirable trends. A major difference of this type of engineering is obvious and crucially departs from geoengineering: since living entities self-replicate, an engineered organism capable of large-

scale dispersal would eventually reach, by growth and reproduction, the desired scale. This could be achieved within reasonably short time scales and the proposal is not limited to capturing carbon dioxide: as an example, engineered bacteria could be designed to help plants facing stressful habitat conditions in order to improve their survival, perhaps enhancing desirable soil microbial communities. Other manipulations affecting photosynthetic efficiency or light-sensing properties could also change the ways we can repair damaged habitats (see below).

The release of a living system that has to spread over large biogeographic areas should be considered cautiously (Snow et al 2005, Pilson and Prendeville 2004). How they can affect community-level traits requires a multi-scale view of ecosystem processes (Whitham et al 2006). However, we already know that a harmful invasion of a given community from an engineered species (Sanvido et al 2007) as it occurs with non-engineered ones, is difficult, since multiple barriers need to be overcome (Blackburn et al 2011). We also need to consider that, given the fast progress and cost reductions associated to this technology, it is not too soon to start exploring the set of problems presented here. By its nature, it requires the merging of multiple disciplines and a serious consideration of the tradeoffs between designed forms of life and the evolutionary responses to their introduction. However, a well developed theoretical framework already exists concerning the reliability of ecosystems and the role played by key factors such as species redundancy (Pimm 1991, Naeem 1996). Moreover, it can be argued that there is only one Earth-like planet that we can study and we can easily conclude that the lack of alternative scenarios makes the whole proposal highly speculative. However, as discussed below, not only one, but many case studies might actually be available to us, and much closer than one would expect.

Several differences can be noticed while comparing the Mars Terraforming scenario and the one considered here. Mars requires a bottom-up development of a resilient network of biotic-atmospheric interactions enhancing life. That means a sequential process of niche construction, where cells adapted to the extreme conditions of the new planet must be capable of modifying this environment in order to grow in increasingly more efficient conditions. Under these conditions, evolutionary dynamics is on our side: selection for more efficient metabolic pathways, better protection mechanisms against radiation and climate extremes would spontaneously trigger improvements. In our planet, bioengineering would be a more top-down strategy, since the network of existing species and their biogeochemical context is already established. Engineering new species means to redefine the existing network of interactions so that we can restore previous steady states or perhaps create novel ones. That would require building new symbiotic relations with existing species and considering several facets of the synthetic one, from efficiency to evolvability.

Synthetic ecosystems

The proposal described here departs from the assumption that a synthetic organism can act, in some circumstances, as ecosystem engineer (Jones et al 1994) capable of modifying the existing balances energy and/or nutrient flows. In nature, bacteria and microscopic algae in particular have played a major role in shaping our Earth's climate (Kasting and Siefert 2002, Falkowski et al 2008, Lenton and Watson 2011) and could help us restore lost balances. Such interaction might have created a stable homeostatic robustness, as formulated in Lovelock's Gaia hypothesis (Lovelock 1992, Lovelock and Margulis 1974, Lenton and van Oijen 2002). This view suggests that negative feedbacks control departures from the range of parameters facilitating life, although other views suggest that positive, destabilising feedbacks might be no less important (Ward 2009, Field et al 2007). But there is little count that humans too have been effectively operating as ecosystem engineers (Vitousek et al 1997) by adapting the biosphere to their needs, while expanding their

populations in a hyper exponential fashion. Because our long-term influence, vast amounts of energy-intensive fossil fuels have been used to power our civilisation, reinforced by the accelerated growth of agriculture from the Neolithic revolution. Profound alterations of the water and nitrogen cycles are a direct consequence of these unsustainable practices. Moreover, an ongoing rearrangement of biotic systems has been taking place, mainly due to habitat loss and biological invasions (Elton 1958, Drake et al 1989). By doing that, we are changing the face of our biosphere, placing ourselves close to a planetary-level critical transition. Can the situation be reverted?

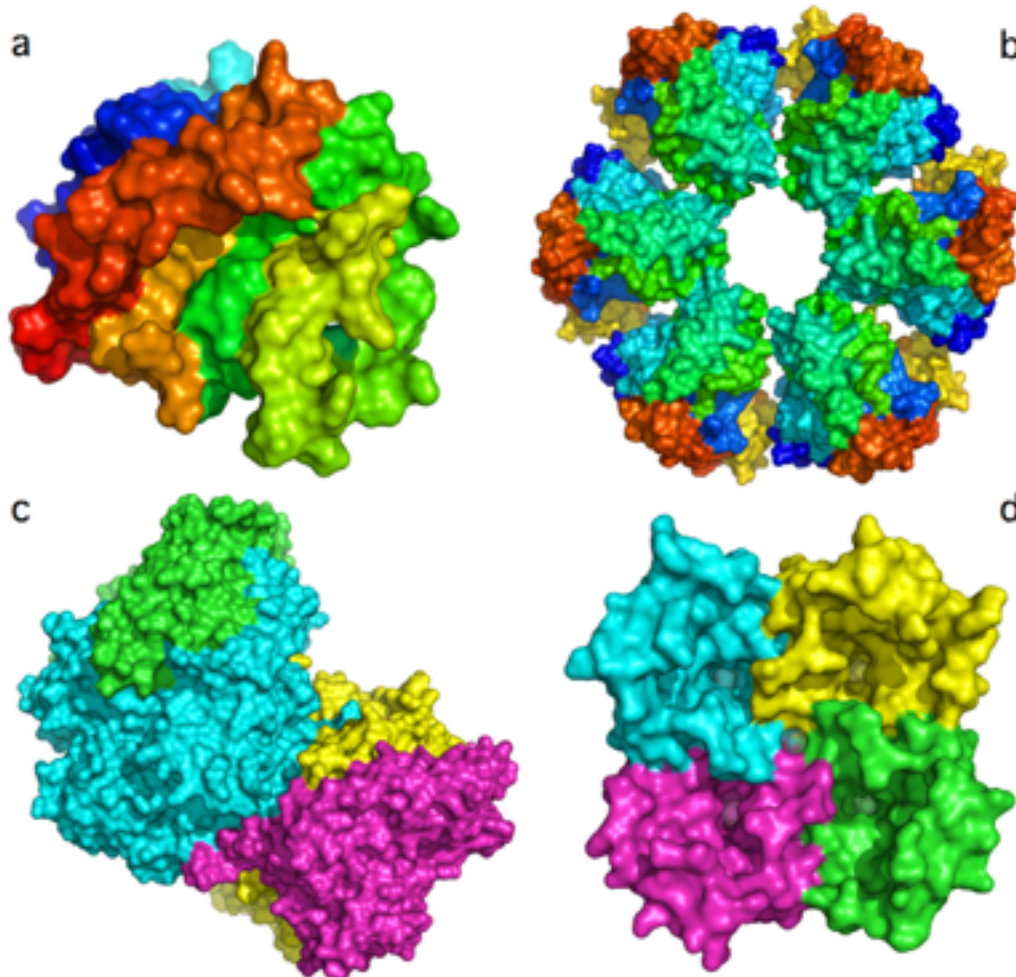


Figure 1. Engineering of molecular structures allows to overcome limitations to metabolic efficiency, water shortages and nitrogen fixation. Here we show the molecular structures of (a) phytochrome, used by plants as a light detector molecule, which has been modified in such a way that photosynthetic processes and growth can take place under shading. In (b) we display the Rubisco complex of Tobacco, the key enzyme associated to CO₂ assimilation. By knocking out the gene associated to this enzyme and introducing the one from a cyanobacteria species, higher efficiency was achieved. A third example is the enzyme nitrogenase (c) which is used by Bacteria and Archea for nitrogen fixation. In (d) we display the Aquaporine 1 transporter protein, which can help improving water use efficiency. The 3D pictures have been created using the Pymol software package for molecular visualization (<http://www.pymol.org>).

Consider the following situation. A given environmental variable needs to be restored by means of a proper intervention based on a modified microbe or engineered plant species, which will act (effectively) as a designed invader. On a small or regional scale, this perturbed system can be a contaminated terrain or a degraded semiarid land. On the largest scale, reducing greenhouse gases or nitrogen excess in open sea would define two major problems. Concerning the first scenario, bioremediation strategies have been already ad-

dressed since the mid 1980s mostly associated to organic pollutants or heavy metals, with different degrees of success (Cases and de Lorenzo 2005, de Lorenzo 2008). A major obstacle to evaluate their potential in the field is, of course, related to biosafety issues. New methods from synthetic biology are changing the landscape (Sayler and Ripp 2000). The area has been useful to understand the interplay between metabolic-level constraints and ecological-level (population) factors. Many problems arose when using strains of modified bacteria due to poor responses to environmental stress, reduced selective advantage associated to accumulated waste products and unpredictable factors resulting from a poor understanding of physiological traits. In other words, modified genetic and metabolic networks were not enough: as it occurred with PCB-degrading strains with all the genes required for it but nevertheless failing to do the biodegradation as expected. Predictive power has increased thanks to genomic search, along with systems and synthetic biology approximations (Schmidt and de Lorenzo 2012).

Synthetic biology represents the last step in our potential for modifying natural systems. The field has been growing fast in the last decade and has emerged as an engineering approach to modify or even create *de novo* living cells tissues and organs (Purnick and Weiss 2009, Khalil and Collins 2010) and is considered a promising new framework capable of facing a large array fundamental problems, including new therapies, development of drugs or biofuel production (Wang et al 2013). Different approaches have been taken to modify living entities or even create new ones from scratch (Solé et al 2007a, 2007b). Among them, two main paths are being followed. One is the top-down approach, where we start from an already existing species and modify it. This path is being followed by research projects involving the reduction of genomes and the concept of a minimal gene complement (DeWall and Cheng 2011). Minimal genomes are characteristic of both free-living and endosymbiotic species (McCutcheon and Moran 2012) but free-living microbes can also exhibit a reduced genome, as illustrated by the cyanobacterium *Prochlorococcus*, one of the most abundant marine microbial genus (Dufresne et al 2003). Despite not as well developed as with *Escherichia coli*, libraries of genetic constructs (so called biobrick parts, see Wang et al 2012) for cyanobacteria are already available (Baker et al 2006). Although most efforts in this area have been directed towards the synthesis of biofuels and other chemicals, improved CO₂ fixation and light harvesting have also been achieved (Ducat et al 2011). In this context, a widespread microorganism containing a minimal genome appears to be an optimal candidate towards engineered carbon sequestration in the ocean.

The synthesis of a whole bacterial genome dramatically showed that a large-scale, genome-level engineering is feasible (Gibson et al 2008) although we need to accept that little is really known about how genes actually interact in a whole network. Genome reduction is still under development but it will surely deliver reliable designs in a near future (Esvelt and Wang 2013). The bottom-up approach to minimal cells includes the creation of protocellular systems (Szostak et al 2001, Rasmussen et al 2008, Luisi 2006, Solé 2009) up from pure chemistry, not necessarily the biological one, thus requiring to cross the twilight zone separating living from non-living matter. This achievement has not been successful so far, but it is not unlikely to happen in a near future. A great advantage of this approach is that designed protocells might be more easily controlled. They can even be much less constrained in their evolvability, while be very efficient in performing a given metabolic function over a range of conditions (Zhang et al 2008). This possibility has been discussed within the context of large-scale bioremediation strategies. An example is provided by the suggestion of using large artificial limestone reefs acting as the physical substrate for synthetic protocells that would be programmed to improve water quality in contaminated or oxygen-poor aquatic ecosystems. Although still a speculative arena, tentative ways of using protocellular constructs combined with artificial reefs have been outlined (Armstrong and Spiller 2010). In these still speculative case studies, both the reef and the microbial population would grow and self-regulate each other.

The use of plants (mostly crops) as the targets of engineering complements the previous single-cell species scenarios. Crop development, selection and geography expansion has been by far the largest ecological engineering process performed by humans. Plant domestication led to highly enhanced yields and a revolution in human history, powering the exit from the Holocene (Diamond 2002). Nowadays, genetic engineering techniques have enormously accelerated the potential for rapidly modulate endogenous metabolic pathways through multi-gene transformation (Palumbi 2001, Zorrilla-López et al 2013). Similarly, sensible improvements to metabolic efficiency and environmental sensing have been overcome (figure 1a-d). Alternative carbon-fixation routes (distinct from those associated to the Calvin cycle) have been elucidated and offer new ways to improve them (Farre et al 2014). Recent work has shown that it is possible to transfer the genes from cyanobacteria coding for the Rubisco enzyme into plant crops (Ducat and Silver 2011) leading to higher rates of carbon fixation (Lin et al 2014).



Figure 2. Bioengineering existing ecosystems will require a proper choice of the kind of model organism to be engineered. Potential organisms could be for example (a) bacteria (here we show *E. coli* cells, from http://en.wikipedia.org/wiki/Escherichia_coli) that could be programmed to perform specific functions or (b) engineered plants (here genetically transformed *Solanum* plants, from http://en.wikipedia.org/wiki/Genetically_modified_crops). Moreover, very different scenarios can be considered in relation to where these modified organisms can be released. This can include man-made substrates, such as (c) marine debris (image from http://en.wikipedia.org/wiki/Marine_debris) and also (d) arid and semi-arid ecosystems (picture courtesy of S. Valverde). In both cases, a combination of genetic firewalls and habitat constrains would help to contain engineered organisms.

Other breakthroughs of molecular engineering might introduce a powerful twist. An example is the modification of plant phytochrome (Whitney et al 2011). This light-sensing molecule is a crucial component of plant physiology, acting as a light detector that triggers plant responses to given levels of sunlight. Decreased radiation input leads to a less active state. However, that threshold response could be tuned, in prin-

ciple, by changing the molecular switch (Burgie et al 2014). A third example involves the enzyme nitrogenase, which has been used to improve nitrogen fixation in cereals. Although molecular nitrogen accounts for the largest fraction of atmospheric gases, it cannot be directly fixed by plants. Instead, this limitation is circumvented in agriculture by chemical fertilisers, resulting in greenhouse gas production and damage to aquatic ecosystems through eutrophication as well as other environmental problems (Canfield et al 2010). The possibility of designing synthetic plant-microbial consortia capable of fixing nitrogen would represent a major advance. Similarly, advances in the Crassulacean acid metabolism (CAM) suggests that water use efficiency in arid ecosystems could be improved (Borland et al 2011). This can be a specially crucial approach to reduce the future impacts of water depletion (Carnicer et al 2011). Current strategies include engineering key molecules as the CO₂-transporting aquaporin (Sade 2014) or moving CAM into C3 crops.

Predicting the outcome

In order to address the problem of accidental release of modified organisms, protocols for contention appeared as soon as genetic engineering started to develop. However, the early claims of the impact of recombinant DNA technology have been shown to be largely unfounded (Berg and Singer 1995). Synthetic biology has raised similar concerns and different biosafety protocols have been established. In fact, the design of new organisms that perform given functions can include, as part of the new circuits, control components facilitating biocontainment (Wright et al 2012). Metabolic dependencies, programmed cell death, auxotrophic constraints or strict synthetic symbiosis are well known ways of implementing genetic safeguards. In this area, important advances in genetic engineering have been achieved. These include introducing switches that activate once a given external signal moves below a threshold or conditional suicide are well known possibilities (Moe-Behrens et al 2013). Most of these designed mechanisms have been build using prokaryotic species, were higher mutation rates favour evolutionary responses and both failure of the switch and spread of undesirable genetic material are possible outcomes. However, recent work suggests that it might be possible to engineer the evolutionary potential of synthetic organisms (Renda et al 2014). Further improvements and genetic firewalls will be achieved by using eukaryotic species, particularly by working on microbial species with minimal, well characterised genomes as well as plant crops and engineered microbes associated to them (figure 2a-b). But we also need to face a reality: hacking living systems is becoming a cheap and widespread task, as standardisation of genetic parts becomes a reality (Endy 2005, Ledford 2010, Schmidt 2008). Little is known about the potential for survival of these engineered strains nor what ecological-oriented biosafety measures should be used.

Released synthetic organisms can remain locally established when the chosen environment and the habitat constraints make spread to other areas unlikely (figure 2c-d). This can be the case of semiarid ecosystems, which may be largely responsible for CO₂ emissions (Poulter et al 2014). Here the strong limitations to growth due to water shortages and poor soils are in fact a challenge for any introduced species. Because of these strong niche limitations, containment might be simpler than expected, while the overwhelming amount of solar power should be an advantage. Since the most likely scenario might involve manipulating microbial-plant interactions, the mutualistic loop would also help defining a controllable scheme. Beyond natural systems, we can also consider existing structures resulting from anthropogenic activities as a likely substrate for bioengineering. I would suggest two of them: cities and plastic marine debris. Cities are the greatest hot spots of carbon dioxide emissions, hosting more than half of the global population (Grimm 2008). Urban areas represent an enormous substrate for growing and controlling engineered organisms. Urban landscapes represent a major advantage, namely a constant supervision of the synthetic species behaviour, helping in a

constant supervision of their growth and should coexist with current efforts of management of urban ecosystem services (Andersson et al 2014).

Secondly, the so called “Plastisphere” (Gregory 2009, Zettler et al 2013) provides another anthropogenic (but human-free) substrate that can be exploited as a niche for synthetic organisms. Plastic debris has been extensively colonised by marine life forms from microbes to bryozoans, hydroids or molluscs (Barnes 2002). An example of this could be the use of plastic oceanic vortices, where large amounts of long-lived polymers have been accumulating over the 20th century at an accelerated pace, although recent work revealed a much smaller amount of debris than expected (Cózar et al 2013). This actually suggests that there might be already some biotic degradation or removal process at work. Waste reservoirs, in general, constitute a threat but can also be an opportunity to provide the appropriate habitat for synthetic microorganisms. An imaginative bioremediation proposal (http://2013.igem.org/Team:Imperial_College/mainresults) is to engineer adhesion between existing marine bacteria-forming biofilms so that small plastic particles attach to others, forming larger clumps or even plastic islands. The existing polymer habitat could also be used to create a diverse consortium of engineered, cooperating bacteria associated to polymer degradation coupled to enhanced carbon fixation. As a relatively confined spatial system, it would help to monitor the spread and efficiency of the bioengineering process and how robust its development over time.

How can we predict the possible outcome of manipulated life forms in a complex biosphere? What might be the most reliable and safe design to be developed? One avenue should involve the classical approach taken in ecology of using micro- and mesocosm experiments, which have been extensively used in ecological engineering (Odum and Odum 2003, Stewart et al 2013). These are spatially confined, carefully controlled laboratory habitats where temperature, humidity and nutrient intake are tuned, while the ecosystem responses are monitored. Many experimental protocols associated to plant engineering match this description. Additionally, mathematical and computational models should be used, including available information and capable of making forecasts across multiple scales (Woodward et al 2010, Evans 2011). Another place to address our previous questions lies inside us, in the so called human microbiome (Huttenhower et al 2012). The host-microbiome network of interactions is the outcome of a long co-evolutionary process and seems to be essential in maintaining organismal homeostasis (Dethlefsen et al 2007). It defines a complex web of interacting species, whose links are strongly influenced by ecology and geography (Smillie et al 2011). Perhaps not surprisingly, the biodiversity patterns displayed by microbiomes have many things in common with the regularities found in species-rich ecosystems. More importantly, a proper understanding of both the healthy and diseased microbiome requires an ecological-level perspective. In this context, it has been proposed that processes associated to invasion by pathogens can be understood in terms of standard invasion ecology. Treatments and recoveries from disturbance can actually be represented in terms of shifts among alternative states (Costello 2012, Pepper and Rosenfeld 2012). The human microbiome can thus be regarded as a large scale, multispecies ecosystem where both the effects of perturbations and potential recovery scenarios can be traced in detail.

Whether synthetic microorganisms are delivered as free entities, to become part of soil microbiomes or as integrated, symbiotic species within more complex hosts, it will be important to predict the success of these new species as they become part of their new environments and start expanding. This is a major topic within invasion ecology (Elton 1958, Parker et al 1999, Simberloff and Rejmánek 2011, Strayer 2012) where a key question is what makes a new species getting established within a community (Vitousek et al 1996). Predicting invasion success has been addressed in many different ways, using different sources of information, from network structure to morphological traits (Romanuk et al 2009, Azzurro et al 2014). Moreover,

invaders can succeed only temporally, sometimes collapsing into extinction (Simberloff and Gibbons 2004) despite an initial successful population expansion. Since we might be interested in a transient response where the engineered species performs a function, such so-called boom-and-bust cycles might be the appropriate dynamical targets. It is also worth noting that the initial impact of invaders can decline in the long term, with species richness and productivity restored after a few decades (see for example Dostál et al 2013, Strayer et al 2013). A rule of thumb is that a successful invader has to be capable of occupying some available niche space not exploited by the members of the receptor community (Shea and Chesson 2002). Are there equivalent rules of thumb for bioengineered systems? Future developments towards a theory of synthetic invaders will require to address the problem of how to define the niche requirements of the designed species in order to succeed.

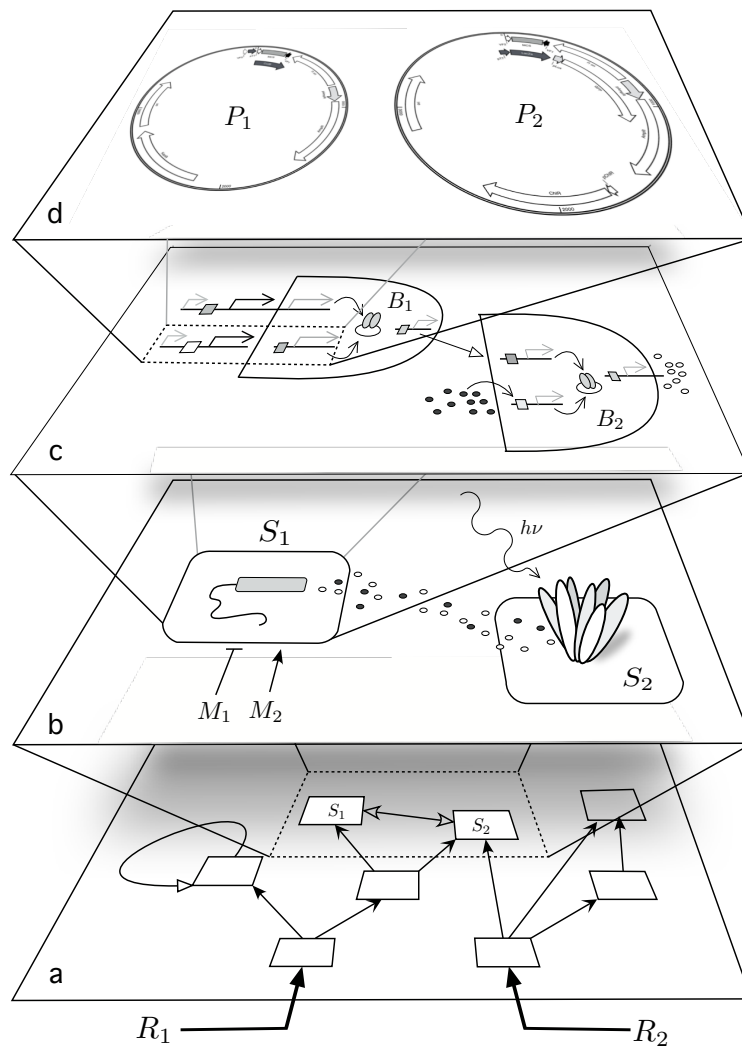


Figure 3. A systems view of bioengineering ecosystems using synthetic biology. Multiple scales need to be considered in order to design a given functionality to be embodied within a given ecological web. From bottom to top, we have (a) the ecosystem level, where the web of interactions among species (S_k) and external inputs and resources (R_k) needs to be considered, along with biogeochemical constraints, (b) the species interaction level, which can involve multiple kingdoms and different kinds of relationships, particularly mutualistic ones, and where a given species might be affected (modulated) by external signals (M_k), (c) the single-species design circuitry to be modified by genetic engineering of specific logic blocks (B_k) and (d) the molecular toolkit (which involves, for example, molecular constructs on plasmids, here indicated as P_k) used to engineer the specific molecular machinery and regulatory interactions.

Conclusions and discussion

What can be the impact of terraforming our own planet? Should we even consider that possibility? Can we deal with the complexity associated to such scenario? Some have compared geoengineering approaches to climate remediation with the Manhattan project (Michaelson 1998) but I think the right dimensions in terms of the challenge are better met with the proposal outlined here. An intervention that can modify the biosphere in controlled ways to reach a new steady state compatible with a planet where humans can live should be seriously considered and joint international efforts might be required at some point. Beyond the technical challenges (that might require a war-level effort) and the much needed theoretical basis, the problem of how decisions should be adopted at the regional and global scales, and whether consensus is even achievable, is part of the scenario presented here. As it occurs with geoengineering (Schneider 2008) global cooperation would be required. Nevertheless, what seems clear is that the tools for building some of the candidate organisms discussed above will be available sooner than later and not necessarily coming from academic institutions (Church and Regis 2012, Porcar and Peretó, 2014). A “domesticated biotechnology”, as defined by Freeman Dyson (2007) implies an enormous combinatorial power. We should not wait to start thinking about the ecological effects of new organisms as potential invaders. Instead, designs and strategies favouring successful, but limited, establishment should be started to be tested as soon as possible.

This paper does not systematically consider all the alternatives. I have not mentioned viruses, for example, as potential targets of bioengineering designs. One reason for this exclusion is that viruses are the most rapidly evolving part of our biosphere and thus genetic firewalls might face serious challenges. However, they are also a major driver of global geochemical cycles (Wilhelm and Suttle 1999, Fuhrman 1999) strongly influencing ecological processes in the ocean (Suttle 2005). Moreover, our view of viruses as parasites or pathogens has been shifting over the years as they play a beneficial role in many different associations with species belonging to all kingdoms (Roosinck 2011). Since mutualistic links might constrain their evolvability, engineered viruses should not be discarded. Similarly, other symbiotic relationships could also play a role once we fully develop the right engineering tools. This is the case of synthetic chloroplasts (Agapakis et al 2011) by introducing engineered photosynthetic bacteria within animals. Similarly, we should not exclude the use of xenonucleic acids (XNAs) where novel informational biopolymers are used (Schmidt 2010). Unconventional ways of strongly limiting spread and evolution can also be obtained by using cell consortia (Brenner et al 2008) where different cells involving different engineered parts perform together a given function, including cooperation (Shou et al 2007). A non-standard approach has been shown to provide a source of modular design while strongly departing from both biological and engineering principles (Regot et al 2011, Macía et al 2012). In this so called “distributed multicellular computation”, the requirement that all parts must work altogether automatically places constraints to evolution and spread. Moreover, this class of so called cellular computing (Amos 2004) is grounded in a design scheme that does not follow standard engineering approaches. It is instead closer with the ways biological systems manage information in a distributed fashion (Solé and Macía 2013).

We cannot foresee all future changes that will unfold in the next decades as a consequence of our impact. What we do know is that all sorts of evidence point towards an unsustainable outcome where our society is likely to fail unless serious measures are taken (Brown et al 2011). Novel approaches are needed, and often the novelty emerges at the crossroads between apparently distant fields. Nowadays, synthetic biology and ecological theory are loosely connected, but it is at the intersection between these two major disciplines where some solutions might reside. The essential message is that we need to reinvent a small part of

nature in order to preserve as much as possible while we guarantee our persistence as a species in a sustainable way. To reconnect with the biosphere, we might need to redesign it, but using a multiscale, complex systems view of ecological systems (Figure 3). In this context, useful lessons can be extracted from controlled field experiments involving species additions or removals and the consequent trophic cascades (Brown and Heske 1990, Estes et al 2011). Similarly, a variety of model approaches will be needed, from simple population-nutrient flow models involving differential equations (DeAngelis, 2013) to large-scale models of climate and bio-geochemical cycles (Lenton et al 2007). The later would be useful to explore the impact of tentative strategies of carbon sequestration, providing some clues concerning the expected C:N:P stoichiometric ratios resulting from bioengineering. Here too some basic models (Klausmeier et al 2004) and a proper choice of target model organisms among the available functional diversity (Arrigo 2005) will be essential to develop this framework.

The fact that we are proposing an engineering perspective does not mean that we can change ecosystems in whatever way we wish. As ecologist E. O. Wilson stated, this is “one planet, one experiment” (Wilson 2010) and our first obligation is to scientifically evaluate any artificial modification scheme. No one should get the message that we “give up on the Biosphere”. Instead, we need to improve our knowledge on how complex ecosystems work, while considering possible interventions and adopt them under international agreements. A better understanding of how and ecosystems decline is needed in order to drive future research in this (still to be defined) field. In this context, the study of novel ecosystems resulting from human action, climate change and other accidental or deliberate events is by no means new (Hobbs et al 2006, Seastedt et al 2008, Hobbs et al 2009, Lurgi et al 2012). Lessons from past species invasions and their long-term effects should actually guide us in extracting useful lessons and some cautionary tales (Strayer et al 2006, Sax et al 2007). We can use this knowledge to intervene in ways that preserve both biodiversity and human well-being. Some key ideas from a complex systems view of ecosystems should guide us (Levin et al 1997, Levin 2000, Solé and Bascompte 2006) and our design efforts must be driven towards bioengineering reliability (Holling 1973, Peterson et al 1998). Technological solutions must be developed in parallel with strategic decisions including sustainable growth, a proper use of energy and material resources and species conservation. Unless we maintain all parallel efforts to slow down our impact on the Biosphere, no safe way out from the Anthropocene will exist. The challenge ahead is enormous and the scenario presented here must not be taken as a free lunch view of ecosystem remediation based on a blind faith in the success of technology. Instead, it should be seen as a rational framework to help escaping from an ongoing runaway effect, at least temporally. If anything, we certainly are running out of time.

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