

Spatial energetics:

A thermodynamically-consistent methodology for
modelling resource acquisition, distribution, and
end-use networks in nature and society

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A thesis presented for the degree of
MsC Environmental Science
(by Research)



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Abstract

Resource acquisition, distribution, and end-use (RADE) networks are ubiquitous in natural and human-engineered systems, connecting spatially-distributed points of supply and demand, to provide energy and material resources required by these systems for growth and maintenance. A clear understanding of the dynamics of these networks is crucial to protect those supported and impacted by them, but past modelling efforts are limited in their explicit consideration of spatial size and topology, which are necessary to the thermodynamically-realistic representation of the energetics of these networks. This thesis attempts to address these limitations by developing a spatially-explicit modelling framework for generalised energetic resource flows, as occurring in ecological and coupled socio-ecological systems. The methodology utilises equations from electrical engineering to operationalise the first and second laws of thermodynamics in flow calculations, and places these within an optimisation algorithm to replicate the selective pressure to maximise resource transfer and consumption and minimise energetic transport costs. The framework is applied to the nectar collection networks of *A. mellifera* as a proof-of-concept. The promising performance of the methodology in calculating the energetics of these networks in a flow-conserving manner, replicating attributes of foraging networks, and generating network structures consistent with those of known RADE networks, demonstrate the validity of the methodology, and suggests several potential avenues for future refinement and application.

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I declare that this thesis is my own work, except where explicit reference is made to the work of others, and has not been submitted for another degree at Lancaster University or any other institution.

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1. Introduction

The processes of physical resource acquisition and distribution within a system, such as an organism, community, or ecosystem, play a fundamental role in shaping the behaviour and properties of the system as a whole. The types and quantities of resources that a system requires, and what is available to it, drive both its efforts to obtain those resources and the measures with which it allocates them between maintenance and different expressions of growth and development (Ulanowicz, 2003). Considerable effort has been invested in studying the properties, such as scaling (e.g. West et. al., 1997; Banavar et. al.; 1999, 2010), resilience (e.g. Holling, 1973; Callaway et. al., 2000; Gao et. al., 2011), and optimisation (e.g. Dandy et. al., 1996; Prasad and Park, 2004; Gen et. al., 2008; Falke et. al., 2016) of the resource acquisition, distribution, and end use (RADE) networks in a diverse array of natural and human-engineered systems. Less attention has been paid to the explicitly spatial modelling and representation of RADE networks in ecological and socio-ecological systems, however. Spatial scale is a key consideration in the interpretation and applicability of models of these systems (Wiens, 1989), especially when accounting for size-related energetic costs (Jarvis et. al., 2015), or scale-dependent effects of environmental factors such as land use change (Verburg et. al., 1999). Furthermore, characteristics of underlying spatial topology have been shown to have a significant impact on the structural dynamics of networks (e.g. Kosmidis et. al., 2008). The majority of network analysis, especially for natural systems, focusses on interactions between components in the network, however, without clear consideration of spatial distance between these components, and its effect on the processes occurring across the network. This limits the realism, accuracy, and applicability of these analyses. Given the ubiquity of RADE networks, and how they direct and constrain the functioning of systems as a whole, their accurate modelling and analysis is crucial for our ability to understand them and thus protect those supported and impacted by them.

1.1 Generalised Flows

The focus of the work here is on energetic resource flows, as comprised of energy and its mass carrier, though it could be extended in the future to study flows of materials not designed to be consumed specifically for energy, such as water, or even the movements

of people along transportation networks. Although also not addressed in depth here, information, taken to mean the characteristics or values of a process's output (Losee, 1998), plays a vital role in allowing for the existence of these energetic resource flows and determining their efficiency. This information identifies the location, use, and quality of the resource, and can potentially be embodied in the infrastructure through which the resource flows, or coupled with the flow itself. As it would require further study to determine specifically whether information, as defined in this manner, is conserved or obedient to other thermodynamic principles governing physical flows, a full consideration of its role and dynamics is outside of the scope of this work. Its existence as a pre-requisite for the resource flows within RADE networks must be noted, however, especially in the decentralised networks presented later.

In total, then, the energetic resource flows such as those occurring in the networks discussed hereon are a combination of information, matter, and energy. Both matter and energy are unequivocally constrained by their respective conservation laws, and the energy transformations and flows of a system are further directed by the entropy-generation imperative of the second law of thermodynamics. The first two laws of thermodynamics, introduced below, are therefore used in the following sections to discuss the energetics of these RADE networks in natural and human-engineered systems, and to assess the applicability and realism of past modelling efforts with regards to representation of resource flow conservation and entropy generation. Equations based on these laws will also be used to direct the development of the generalised resource flow methodology presented further on.

1.2 Resource Thermodynamics

As with all physical systems, or those with a physical component, the energy flows within RADE networks are governed by thermodynamic laws, which describe the dynamics of energy undergoing transformation processes. In the context of RADE networks specifically, one such transformation is that of energy being expended in the transportation of resources from points of supply to consumption. Energy conversions also take place in biotic and abiotic RADE networks at points of end use, such as the conversion of food via metabolic processes in organisms, although for the purposes herein the energy requirement for transportation is more in view. The thermodynamic

laws governing these transformations are thus key to understanding the impetus and constraints of RADE networks, as the networks both supply energy to points of end use, and require some of this energy to be reinvested in obtaining future resource flows.

Specifically, the first law of thermodynamics states that energy is conserved during conversions between forms, whilst the second states that entropy cannot decrease within a closed system (Kleidon, 2016). This implies that the many energy transformations that occur within a system, such as those described above, produce both useful work and entropy. For example, in a human's metabolic network, energy conversions both perform useful work in transporting and digesting the energy in food, and generate entropy in the form of heat, which is lost to the air. In closed systems, this entropy production would entail that the overall state of the system is one of increasing entropy, progressing toward a state of thermodynamic equilibrium. In thermodynamically-open systems, however, such as the body of a human, the system is able to move energy and mass across its boundaries, thus maintaining a state far from thermodynamic equilibrium by exporting the entropy that is produced by these energy transformations. This also allows for larger-scale open systems, such as the earth system and the many nested ecosystems within it, to maintain an ordered state that is able to support life.

In all RADE networks, both natural and human-engineered, the first law of thermodynamics constrains the quantity of energy within the overarching system, both through energetic resources supplied by the networks to points of end use, and energetic costs of building, maintaining, and moving resources along these networks. As energy is conserved in each transformation, the energy that leaves a RADE network, either through consumption at the point of end use, or as entropy due to frictional losses incurred during transportation, is the same quantity as the energy that originally entered the network. The entropy generated, however, as dictated by the second law, cannot be expended as useful work. Therefore, the net useful energy gain at the points of end use is the total energy input at the points of resource supply, minus the energy required for transportation.

Although perhaps apparent upon examination, the entropy production imperative of the second law also clarifies the importance of consistent and explicit consideration of spatial dimension of the RADE network in question: the energy required to transport resources increases with the distance travelled (Jarvis et. al., 2015), as more energy is

necessary to overcome the increased friction associated with moving resource flows across larger distances. Along with producing useful work in transporting resources, the increased energy transformation occurring along larger networks also necessarily increases the entropy production. The spatial size of the network thus determines energetic cost and entropic production, which constrains the net energy throughput of the network within the bounds set by the first law, as described above. Any model of physical RADE networks, therefore, must consistently account for these size-related losses in order to accurately portray the diminishing return to scale caused by network expansion, due to the increased energetic expenditure in transportation, despite the introduction of new resource flows into the system.

As physical growth increases the distance resources must be transported, hence the energetic cost of transport, expanding networks are under constant pressure to increase the efficiency and throughput of their RADE efforts. It has been argued that natural selection favours systems that are able to capture the maximum free energy, or energy available to do work, for their own purposes, and use this free energy to increase their organisation, structure, and therefore distance from thermodynamic equilibrium (Boltzmann, 1886; Lotka, 1922; Schrödinger, 1992). Furthermore, the frequency of structures suggested to be optimal in minimising energy required for transporting materials (West et. al., 1997) would suggest that maximising energetic consumption is achieved in part by minimising the energetic cost of transportation. For this reason, many models of RADE networks in ecology are expressed as an optimisation (Ward et. al., 2000), wherein the energy-gatherer makes ‘optimal’ decisions based on a certain currency, such as maximising energetic efficiency, or rate of energy consumption, with efficiency used as a proxy for maximising consumption and minimising associated energetic cost. Empirical evidence to the same shows that many species follow optimal foraging patterns of Lévy flights (Reynolds et. al., 2007), a random walk structure in which the distribution of path lengths is heavy-tailed such that shorter paths are more frequent than longer moves. It is argued that permanent physical RADE networks follow the same directive to maximise their resource consumption and minimise their energetic costs, and the prevalence of highly efficient resource distribution structures such as hierarchical branching networks (Banavar et. al., 1999), in both natural and human-engineered systems, would suggest that this is indeed the case.

1.3 Biological and Ecological Systems

In order to be consistent with the entropy production mandate of the second law of thermodynamics, while maintaining a living state with a high degree of order, a biotic system such as an organism or ecosystem must constantly receive inputs of external energy. These inputs are then coupled with other processes that increase or maintain order, such that the net effect of the process is still one of increased entropy creation and export, despite the local minimisation of entropy within the system (Kleidon, 2016). This imperative to collect and use or store energy is the underlying basis for the ubiquity of RADE networks in living systems, and the aforementioned minimisation of losses is theorised to cause their remarkably similar structures across such systems (West et. al., 1997), although to date that has not been explored explicitly from a thermodynamic view. These networks take the form of both internal resource distribution networks, as occurring within the body or structure of an organism, and external acquisition and distribution efforts of organisms and groups. Although these networks are closely linked and nested, research typically focusses on one or the other as a boundary of the system under question, or on subnetworks within these.

A considerable body of work focusses on the metabolic networks of individual organisms, which has given rise to the so-called Metabolic Theory of Ecology, positing that the metabolic rate of organisms acts as a governing rate of most observed ecological patterns (Brown et. al., 2004). This work began with the discovery by Kleiber (1932) of the sublinear scaling between mass and metabolism, which he later found persists across organisms covering twenty-one orders of magnitude (Kleiber, 1947). The basis for this sublinear metabolic scaling was further explored by West et. al. (1997) and Savage et. al. (2004, 2008), who determined that the observed scaling exponent between mass and metabolism could be caused by the self-similar hierarchical branching, or fractal structures, which comprise the vascular systems of both animals and plants. The value of the scaling exponent takes the form of $D/(D+1)$, where D is the dimensionality of the space filled by the network, hence the observed $\frac{3}{4}$ exponent in three-dimensional organisms. West et. al. (1997) used the same mathematical argument to predict scaling exponents with multiples of $\frac{1}{4}$ in other organismal characteristics, including heart rate, respiratory rate, lifespan, and the size of different vascular network structures. Furthermore, Brown et. al. (2004) has successfully applied this quarter-power exponent

to predict population-level characteristics, including population growth and density, and species distribution. Later work by Banavar et. al. (2010) showed that the same D/(D+1) scaling exponent could be achieved in both fractal and non-fractal networks by scaling the velocity of the flow through them. The demonstrated predictive power of this scaling exponent shows that the structure and/or flows within inter- and intra-organism metabolic networks are key drivers and constraints on the properties and state of the system in question. As the uptake and distribution of required resources is a rate-limiting factor in the maintenance and growth for all systems (e.g. Sebens, 1982; Sterner & Elser, 2002; Garrett, 2011), it is unsurprising that the structures and flows of the networks facilitating these uptake and distribution processes would be such a strong predictor of so many system characteristics.

The importance and impact of RADE networks on the functioning of the entire system, and neighbouring systems, is perhaps demonstrated most clearly in situations of heterogenous resource supply, due to failure of the network, or excess or lack of available resource supply in the surrounding environment. In the case of resource limitation, this constraint feeds back into the distribution network, leading to a wide expression of adaptation in the system in question. For example, it has been theoretically proven that mismatches between resource supply and demand can lead to deviations from the aforementioned $\frac{3}{4}$ scaling between mass and metabolism (Banavar et. al., 1999). This has been empirically demonstrated in several cases, such as that of phytoplankton exposed to growth-limiting irradiance (Finkel et. al., 2004). Similarly, an abundance of resources can cause an organism to adapt its RADE network and therefore overall structure to better take advantage of the supply: the morphological and physiological plasticity of tree roots is an example of such (e.g. Hutchings & Kroon, 1994; Hodge 2004; Ostonen et. al., 2017). These systemic changes, resulting from adaptations of RADE network structures and flows in response to resource supply, represent a fundamental shift in the dynamics of the internal resource distribution and allocation of the organism in question, as it adapts to the constraints on its performance, and re-partitions the resources it can access accordingly. These feedbacks between resource supply and RADE network structure and flow further underscore the importance of accurate modelling, as it will allow for better quantification of network state and therefore system state under different conditions. Although more complete biological and ecological models do consider the impact of resource supply, it is usually

within an interactional model such as a food web (Jørgensen, 2008), as opposed to an explicitly spatial one, though the latter is arguably better equipped to calculate and represent structural network changes, and the energetic costs and constraints related specifically to heterogenous spatial distribution of resources.

These organismal-level RADE networks are nested in larger networks of which the given organism is but a part. The dynamics and structures of networks on each trophic level play a driving and constraining role on one another, and on neighbouring networks within the same trophic level. For example, the earthworm *C. elegans* has been shown to follow a maximally informative search strategy while foraging, making decisions based on previous knowledge of typical food distribution in its environment, thus adapting its search behaviour to optimise resource acquisition in a heterogenous environment (Calhoun et. al., 2014), mirroring the previously discussed adaptations of internal distribution networks. These earthworm foraging networks, in turn, have been shown to affect plant root foraging and plant growth (Jouquet et. al., 2006; Cameron et. al., 2014), an increase of which leads to increased carbon in the soil (Blagodatskaya et. al., 2014). Changes in soil stoichiometry cause microbial communities to adapt their carbon use efficiency, with implications for soil carbon sequestration, atmospheric CO₂ release, and flows of carbon throughout the entire ecosystem (Sinsabaugh et. al., 2013; Manzoni et. al., 2017). These and similar patterns of interaction between RADE networks across different trophic levels increase their complexity, but also the importance of accurate model development, as changes within one part of the network can have non-localised impacts on a range of spatial and temporal scales.

In many instances, these RADE networks can be represented in physical or temporal space, and numerous studies have been undertaken focussing on the latter, examining resource-oriented behaviours such as gathering building materials, hunting, and foraging, in a range of species spanning from earthworms and bees, to large predators (e.g. Hansell, 1984; Scheel & Packer, 1991; Kunkel & Pletscher, 2001; Leonhardt & Bluthgen, 2012; Simard et. al., 2015). The infrastructure comprising these networks are the bodies of the organisms in question, and their paths through space and time to locate and transport resources. Although not always as visible or permanent as vascular systems in animals and plants, these spatiotemporal structures equally represent energy-driven efforts to move resources from points of acquisition to end use, and are thus

subject to the same selective pressure to maximise consumption and minimise energetic cost. As with physically permanent RADE networks, the spatial scale and topology of these structures is a necessary consideration in calculating the energetic cost of traversing them, but most previous work has focussed on the temporal dimension exclusively (e.g. Sinervo, 1997; Ward et. al., 2000). Studying the dynamics, differences, and similarities of these energetic costs to which different types of RADE networks are subject, and the adaptations expressed to minimise them, will improve understanding of how they support their constituent organisms and impact one another, and predict how they will respond under different conditions.

1.4 Human-engineered Systems

Arguably more so than any organism, humans are voracious consumers of energy and physical resources, as evidenced by our vast and complex distribution networks of the same. The interconnection of these networks makes them especially prone to cascade effects from targeted attacks and accidental failures (Wang & Rong, 2009; Buldyrev et. al., 2010), and their necessity for societal functioning as we know it is demonstrated by the widespread pandemonium caused by such disruptions (Kinney et. al., 2005). Some of the most obvious, and hence widely studied, of these networks are those for distributing energy, including the electrical grid, natural gas transmission system, and other distributed systems (e.g. Driesen & Katiraei, 2008; Dalgaard & Strulik, 2011; Nasr & Conner, 2016). As now nearly half of the energy that comes through human-engineered RADE networks is used simply to move resources through the network (Jarvis et. al., 2015), the optimal design and functioning of these energy distribution networks is paramount to the regular functioning of industrial society and the global economy, even before considering expansion efforts. Moreover, the same $D/(D+1)$ scaling exponent between mass and metabolism in organismal metabolic networks has been observed in these global-scale primary energy flows (Jarvis et. al., 2015), suggesting that industrial society not only behaves like a superorganism (Campbell & Stock, 2002), but is also built like one, as the decreasing efficiency of distribution across the ever-expanding network drives efficiency improvements in other areas (Jarvis, 2018), leading to the development of the same fractal branching networks observed in organismal metabolic networks. The frequency of this structure would suggest a level of robustness to its optimality, given the diversity of the systems in which it emerges,

but whether it is optimal for the diverse expression of energetic costs and constraints experienced by different systems, or optimal for a subset of these costs that are experienced by all systems, requires further study.

Closely linked and often interconnected with these primary energy RADE networks is the vast transportation infrastructure of roads, railways, canals, and flight paths, all of which work together to transport energy, people, and other materials (e.g. Bell & Iida, 1997; Guimera et. al., 2005; Samaniego & Moses, 2008). Despite the heterogeneity of flows along these networks, and the terrain through which they pass, they are all subject to same size-related energetic penalties, as the energy required to maintain and traverse them increases with their size (Jarvis et. al., 2015). Careful consideration to the topology, dimension, and size of the space occupied by the network is therefore necessary to accurately quantify these energetic costs and understand the evolutionary constraints. These transportation networks have also been shown to follow the same scaling dynamics between size and flow as the primary energy networks discussed above and in the metabolic networks of organisms (Banavar et. al., 1999), further suggesting that these dynamics may be driven by a common imperative. The robustness of this phenomena across diverse networks has been further evidenced by recent successful uses of slime mould *P. polycephalum* to model national transportation networks of countries around the world (Adamatsky, 2012), an outcome that only makes sense under the framework of seemingly dissimilar networks expressing a similar response to minimising energetic costs, while connecting a heterogeneous distribution of resources and points of end use.

The dynamics and flows of these man-made distribution networks, and therefore necessarily the spatial distribution of the resources and people that they transport, have also been linked to scaling dynamics in characteristics of the cities and communities they support (Kühnert et. al., 2006; Bettencourt et. al., 2007; Bettencourt, 2013). The physical and influential reach of these networks, as well as their considerable impact on the surrounding and supplying environment (Alberti et. al., 2003), merits the importance of understanding and modelling them accurately. Multi-vector energy systems analysis (e.g. Carradore & Turri, 2009; Devlin et. al., 2017), which incorporates multiple, diverse energy sources, and coupled socio-ecological systems analysis (Polhill et. al., 2015), which attempts to account for impacts from both natural and human-engineered

dimensions of systems, are two areas that are especially attracting attention recently, as the interconnection of the many levels of RADE networks in these systems entails necessary transfer of energy and materials across the boundaries typically drawn around each by their respective disciplines.

1.5 Modelling RADE Networks

In order to better understand the structures and flows of RADE networks, quantify their energetic costs and environmental impact, and improve their resilience, sustainability, and equity, the ability to model them comprehensively and accurately is essential. Models of RADE networks or aspects of them abound in the literature, from systems of equations describing electrical power or water flow (e.g. von Meier, 2006; Yazdani & Jeffrey, 2011), to the aforementioned foraging energetics models. While each has insight to offer, many are lacking in one or more features that could be offset by combining elements of models from different disciplines, to create a more comprehensive depiction of the system under analysis, and a generalisable model of resource distribution dynamics.

Models of RADE networks in ecology and biology are often in the form of mathematical, interaction-based models without explicit consideration or representation of the effect of spatial size or distance between points of resource supply and demand. Most ecological network analysis focusses on producer-consumer interactions and analyses using the resultant adjacency matrix of relationships and rates of production and consumption, and is hence more temporal and relational than spatial (Jørgensen, 2008; Sibly et. al. 2013). Although these interactions are a key aspect of resource networks, they are but a part, representing the ‘end points’ of the network. Explicit inclusion of spatially-driven energetic costs incurred en route would improve the accuracy of calculation of production and consumption rates, and resulting overall energetics. Similarly, in biological systems, network analysis usually focusses on the relationships and interactions between genes, cells, or proteins (e.g. Barabási & Oltvai, 2004; Zhu et. al., 2007; Ma’ayan, 2011), wherein regulatory signals, substrates, and products are the resources transported between reactions. The predominance of graph theory techniques and concepts in analysing these networks means that most of them calculate distance using path length, or count of unit-length links, as opposed to a

precise spatial distance. The interactional basis of these network models mean that this is an accurate and useful metric, but accompanying spatially-focussed analysis is lacking.

One exception to the predominantly non-spatial network analysis in ecology and biology is that of foraging models, which often involve some form of spatial measurement in order to quantify the energetic costs of foraging (e.g. Bernstein et. al., 1988, 1991; Ward et. al., 2000). Even these, however, sometimes rely on time as a proxy for energetic cost (Sinervo, 1997), which may not be a reasonable assumption depending on the heterogeneity of the landscape (Grünbaum, 1998). Furthermore, most of these models are based on Optimal Foraging Theory, which focusses on a single species or predator-prey pairing, and makes significant assumptions about distributions and probabilities of resources (Kacelnik et. al., 1992), limiting their wider applicability in modelling the holistic dynamics of an ecological or coupled socio-ecological system. Finally, some fail to explicitly consider conservation laws of mass and/or energy, which prevents them from accurately depicting the dynamics of energy and matter flow within ecosystems, as discussed by Lindeman (1942).

A relatively newer technique in ecological modelling that addresses some of these limitations, known as Circuit Theory, applies concepts from electrical circuit analysis to characterise the likelihood of flows between two nodes. It has been applied successfully to assess habitat connectivity, gene flow, and relative habitat resistance to organisms' movements (Gimona et. al., 2012). The end measurement is usually one of 'resistance distance,' which quantifies the inverse of the ease with which a flow occurs between two nodes, taking into account the reduction of resistance from a flow occurring across multiple possible pathways. Although useful for calculating likelihood of flows between different nodes, such as habitat patches or genetic pools, and accurate in its spatial explicitness and conservation of flow, Circuit Theory calculates flows in a pairwise manner, making it difficult to analyse an entire system of nodes simultaneously. It has also been predominately utilised in the domain of habitat conservation and population genetics (McRae, 2006), and received minimal attention in literature on energetic costs and dynamics of resource flow in ecological and socio-ecological systems, despite that the underlying importance of the connectivity that it analyses is fundamentally linked to resource distribution (Taylor et. al., 1993).

Both Optimal Foraging Theory and Circuit Theory models base their descriptions of energetics and movements on the organism in question making optimal decisions, in order to maximise energetic consumption and/or minimise energetic expenditure. This is predicated on natural selection favouring individuals and species that are able to capture more free energy and/or use energy more efficiently, as discussed previously. Over time, therefore, energetically optimal behavioural and movement patterns should emerge. Similarly, the construction and maintenance costs, and the energetic cost of transportation, acts as selective pressure on human-engineered RADE systems, and the emergence of the same network topologies and scaling patterns (e.g. Dalgaard & Strulik, 2011; Jarvis et. al., 2015) would indicate that these networks are also moving toward increasing levels of optimisation. Although modelling RADE networks as fully optimised is a simplification, as the networks are progressing toward a state of optimality with the system constantly self-adjusting and self-selecting in response to environmental changes, it is important to include the influence of selective pressure and progression toward optimisation in modelling networks, especially mature ones.

Along with the electrical circuit analysis from where Circuit Theory derives its equations, spatially-explicit network modelling methods are more common in human-engineered systems, perhaps because the economic cost of spatial coverage is more acutely felt. Modelling efforts of human-engineered RADE networks are typically focussed on the optimisation of one or more aspects of the system under study, such as minimisation of construction and maintenance cost and/or maximisation of reliability and robustness (Cain et. al., 2012). Other models are used to compare the performance of a set system under different operating conditions, to improve predictions of future performance (Herrán-González et. al., 2009). Many of the techniques used to model these networks could prove highly instructive in application to other types of RADE networks, but the interdisciplinary use of these methods is limited. While discussions using terminology previously constrained to the physical sciences, such as free energy, entropy, and power, are becoming increasingly common in ecological and earth sciences literature (see review in Kleidon et. al., 2010), and the rise of complex systems science and notions of self-organisation and complex adaptive systems engage with issues of energy and mass transfer through and across ecological and socio-ecological system boundaries (Levin, 1998; Parrott, 2010), these schools of thought have yet to widely adopt the methodology and techniques used to model similar phenomena in

human-engineered systems. As such, a consistent, general modelling framework for RADE networks has not yet been identified.

It should be noted that studies done on stylised networks such as random or scale-free networks, although verifiably similar in properties to their real counterparts (Albert & Barabási, 2002), generally model the spatial aspect of the network through degree distribution or path length (Callaway et. al., 2000; Gao et. al., 2011). As such, they do not always consistently take into account constraints and costs associated with spatial distance between components, or nodes, which are applicable to all physical networks. While it is often the common purpose, namely the transportation of resources from points of acquisition to end use, that is credited with the remarkable similarity in structure and properties of the diverse expressions of RADE networks, thermodynamic laws play a vital role in directing and constraining the development and flows of all such networks. For this reason, any attempt to model or analyse these networks must account for these laws. Although some of the models discussed above include consideration of one or both of these laws, it is usually sporadic and inconsistently applied, limiting the realism of the model, and its ability to be combined with similar models to predict larger-scale energy flows within natural and human-engineered systems, such as the ecological and socio-ecological systems in view here.

While the stylised networks allow for very neat proofs-of-concept, and can provide many useful insights on the dynamics of general networks, it would be instructive to further validate generalised models such as these by parameterising them to reflect real systems. Even when such parameters are approximate or averages, such as often used in foraging models (e.g. Ward et. al., 2000; Baveco et. al., 2016), the results still provide important overall information on the system under study, that is more generalisable to similar systems, or the same system under different conditions. As these general models ‘sacrifice precision to realism and generality’ (Levins, 1966), they provide insight through simplification, such as overall patterns and directions that would be instructive for further study. Moreover, they provide feedback on the performance of the model, such as whether it can predict qualitative or large-scale features of the networks it was parameterised to reflect, or whether there are clear flaws in the logic or development that prevent its application to real systems. This is similar to the validation method of

populating an ontology with instances, as put forward by Polhill and Salt (2017), to ensure logical consistency in relationships between components in a model.

In contrast to these interactional and stylised models, one subset of RADE networks for which models are especially explicit in their consideration of spatial size and its effects, and the conservation imperative of the first law of thermodynamics, are those of electrical power grids. Using a system of equations that solves for the voltage and current at each node in the network, taking into account the distance-related resistance across the links, engineers are able to calculate the power input, loss, and consumption at points of end use (von Meier, 2006; Glover et. al., 2012). This method, called load flow analysis, is similar to the methods used in Circuit Theory and electrical nodal analysis, as it is based on the same underlying equations, but load flow analysis allows for the calculation of voltage and current simultaneously for all nodes and branches in the network. Despite the potential for these methods to be applied to analysis of flows through other types of networks, the precedent for doing so is minimal: a remarkably similar technique to those used in load flow analysis is used for analysing flows in economic networks, known as Leontief Matrix Inversion (Leontief, 1951, 1986), but to date no one has directly compared the two. Furthermore, in addition to the Circuit Theory examples above, other studies have used equations similar to those in load flow analysis to model information flow in cellular networks (Kim et. al., 2011), but not energetic resource flows. Even though the use of electrical analogues in ecological modelling was pioneered by H.T. Odum in the 1950s (Kangas, 1995), it was applied strictly to performing conservation-based analysis of transfers between and within trophic levels, as opposed to a spatial network analysis such as done in load flow studies. By identifying the analogous voltage, or force, and current, or flux, in ecological and coupled socio-ecological networks, and utilising the advances in computational modelling available today, it is possible to apply the neatly thermodynamically-consistent and explicitly spatial equations of power flow to simulations of full RADE networks of a diversity of types.

1.6 Project Aims

The aims of this thesis are to:

1. Develop a spatially explicit, thermodynamically-consistent framework for modelling generalised RADE networks,
2. Apply an optimisation algorithm to this framework, in order to simulate the selective pressure exerted on RADE networks to maximise energetic capture and minimise energetic costs, and
3. Use the nectar foraging networks of the European honey bee, *Apis mellifera*, as a proof-of-concept to assess and evaluate the network modelling and optimisation.

2. Model Framework

2.1 Operationalising Thermodynamic Laws

In order to accurately model the constraints and influences of the thermodynamic laws discussed above, the laws had to be operationalised to allow for their consistent implementation across both generalised and domain-specific RADE networks. Creating a consistent framework for quantifying the energetic cost of acquisition and/or distribution, or other forms of loss, and including that in calculations of the resource flow produced and consumed in a network, is done in some models (e.g. Huey & Pianka, 1981; Shirmohammadi & Hong, 1989; Wallis DeVries, 1996). This loss term could be used to represent the entropy generation occurring during the energy transformations in RADE processes, such as energy consumption during transportation, or frictional losses occurring as a result of flows of resources along network infrastructure. As discussed above, this entropy generation is required for the model to realistically represent a system involving energy transformations, as the second law of thermodynamics necessitates that these lead to an increase in entropy. Furthermore, as this entropy represents energy that cannot be consumed as useful work, or power, the model must also include this loss to calculate the flows of energy in the network in a way that is energy conserving, as imposed by the first law of thermodynamics. As such, the total flows into the system must be accounted for either as loss due to entropy, or as consumed at the point of end use, with at least some of the energy lost as entropy. Methods have been put forth to calculate flows via least-cost paths or all paths in stylised networks (Carmi et. al., 2008), but neither are suitable for calculating resource flows. Resource flows in both natural and human-engineered systems can occur via multiple pathways, some indirect (Ulanowicz, 2001), necessitating calculation of flow via more than just the least-cost or shortest path. While calculations via all-paths methods are more accurate in this regard, the computational expense is significant for large networks, and the algorithms unwieldly (Migliore et. al., 1990). This would be further aggravated if the network was disconnected, such that the larger network was made up of entirely disjoint subnetworks for which the flows would have to be calculated separately. An alternative formulation is therefore necessary to determine energy-conserving resource flows, along all paths, in a way that accurately accounts for size-related losses.

2.1.1 Load flow analysis

As introduced previously, the methods used by engineers to calculate the voltage and current at each bus and line in a power grid, known as load flow analysis (von Meier, 2006; Glover et. al., 2012), or similarly, the pressure and friction at each head and pipe in a water network, provide an energy- and mass-flow conserving model to calculate the size-related energy and pressure losses across a network. These methods are grounded in the constitutive equations governing the flows of electrical current, a flow of charged particles, and fluid, respectively. These equations are a subset of the phenomenological linear flow laws relating a flux to its conjugate force, where the constant of proportionality between the two, such as resistance or permeability, is a characteristic of the material through which the flow occurs (Plawsky, 2014). These phenomenological laws are all analogous, such that a generalised form of these equations, as based on the second law of thermodynamics, can be used to model any linear physical transport process (Kjelstrup et. al., 2010).

2.1.1.1 Traditional Methodology

Traditionally, the equations used by electrical engineers to quantify the steady-state operation of the power grid are for alternating current (AC) power flow, wherein the electrical charge changes directions periodically, such that the electrical potentials, or voltages, reverse and the flow of current changes directions (Glover et. al., 2012). The equations include terms for both voltage angle and magnitude, and real and reactive power. Although adaptations have been proposed to calculate direct current (DC) power flow, these include significant assumptions, such as lossless lines (Overbye et. al., 2004), making them inappropriate for use when the resistance-driven line losses would be analogous to the size-related energy losses. The methodology for calculating the AC power flow can be adapted more directly to generalised flows, however, by modifying the equations to reflect directed flows, while still including the loss term due to resistance. This is similar to the methods used in modified nodal analysis for calculating the currents and voltages around a closed circuit (Ho et. al., 1975). Unlike modified nodal analysis, however, both load flow analysis and the generalised resource flow methodology presented later on do not require writing out an equation for each node individually, choosing a node to act as ‘ground,’ or eliminating voltage sources, and returns all branch currents.

Both modified nodal analysis and load flow analysis rely on Kirchhoff's current law and Ohm's law to determine the current and voltage of the nodes and branches within the system. In the model presented later on, a generalised form of these laws is used to operationalise the conservation and entropy generation of the first and second laws of thermodynamics. Although Ohm's law was developed deductively (Ohm, 1827), and Kirchhoff's laws as a generalisation of it based on the principles of conservation of charge and energy, later work by Joule (1850) connected Ohm's law more explicitly to the second law of thermodynamics via the heat, therefore entropy, produced by an electrical current. As such, Kirchhoff's and Ohm's laws can be used to represent the underlying thermodynamic laws of conservation of energy and entropy generation, respectively. Specifically, Kirchhoff's first law states that the current flowing into a junction must be equal to the current flowing out of it, due to the conservation of electrical charge (Paul, 2001):

$$\sum_{k=1}^n I_k = 0 \quad . \quad (1)$$

Here, k is the number of links in the junction, and I is the current on the given link. This conservation of the flow of current can be clearly linked to the first law of thermodynamics, which requires the conservation of energy within a closed system, such as the circuit junctions the equation describes, or a closed circuit as a whole. The current in the equation is related to the voltage of the connected nodes via resistance, a constant of proportionality that describes the difficulty presented to an electrical charge by the conductor through which it flows (Paul, 2001). This relationship is described by Ohm's law, which states that the change in voltage across a resistive link is equal to the current times the resistance, R (Paul, 2001):

$$\Delta V = IR \quad . \quad (2)$$

This 'voltage drop' and the resulting power loss between the origin and destination of current flow, represents the loss of energy that could be used to perform work, and hence the increase of entropy, within the circuit. As used in load flow analysis, equations derived from Ohm's and Kirchhoff's laws allow the engineer to determine the voltage magnitude and phase angle for each power generating (generator) or receiving (load) bus, and the current along each link (branch) in the network (Glover et.

al., 2012). It is assumed that the voltage magnitude and power generation at generator buses, and the real and reactive power demands at the load buses, are known. Additionally, one generator bus is chosen as the slack bus, for which voltage magnitude and angle are known, and is used to generate any mismatch in power demand and supply within the system. This allows the engineer to develop a system of equations to solve for the unknown voltage magnitude and angle at the load buses, and voltage angle at the generator buses. A full overview of load flow analysis is provided by Glover et. al. (2012), but is summarised here to clarify the origin of the modifications used in the generalised model presented later, which uses similar equations to calculate the force and flow of resources in a generalised RADE network.

Load flow analysis begins by constructing an admittance matrix for the network, which specifies the admittance between each bus, with the diagonal elements of the matrix containing the self-admittance, or a negative of the sum of all admittances for that bus. Admittance, Y , is the inverse of impedance, a complex number which takes into account both the resistance, opposition to a steady flow of current, and the reactance, opposition to a change in current. As such, admittance represents the ease with which alternating current can pass through a resistor,

$$Y = G + jB, \quad (3)$$

where G is the conductance term, and B is the susceptance. j is the imaginary term, where $j^2 = -1$. After constructing the admittance matrix, initial estimates are made for the unknown variables listed above at each bus. The mismatch between the known values listed above, and their calculations based on these initial estimates, is determined using the power flow equations. The power flow equations calculate real and reactive power through application of Ohm's law:

$$P_i = \sum_{k=1}^n |V_i| |V_k| G_{ik} \cos \theta_{ik} + B_{ik} \sin \theta_{ik}, \quad (4a)$$

$$Q_i = \sum_{k=1}^n |V_i| |V_k| G_{ik} \sin \theta_{ik} - B_{ik} \cos \theta_{ik}, \quad (4b)$$

where P_i is the real power at bus i , Q_i is the reactive power, $|V_i|$ and $|V_k|$ are the voltage magnitudes at buses i and k , and θ_{ik} is the voltage phase angle difference between buses i and k .

There are two main methods to solve for these equations at each bus: the Gauss-Siedel method, and the Newton-Raphson method, the latter of which is more commonly used today. In the traditional Newton-Raphson method, the mismatches between known and estimated values for real and reactive power at each bus, as calculated by Eq. (4a) and (4b) above, are used with a four-part Jacobian matrix of partial derivatives of both real and reactive power, each with respect to voltage magnitude and angle, to form a system of equations expressed as:

$$\begin{bmatrix} \Delta\theta \\ \Delta|V| \end{bmatrix} = -J^{-1} \begin{bmatrix} \Delta P \\ \Delta Q \end{bmatrix}, \quad J = \begin{bmatrix} \frac{\partial P}{\partial\theta} & \frac{\partial P}{\partial|V|} \\ \frac{\partial Q}{\partial\theta} & \frac{\partial Q}{\partial|V|} \end{bmatrix}. \quad (5)$$

The system is then solved to produce $\Delta\theta$ and $\Delta|V|$, which are used to update the initial estimates for voltage magnitude and angle at the load buses, and voltage angle at the generator buses. The mismatch is calculated again, and the process of solving the system of equations and updating the estimates is repeated until the mismatch is within a pre-defined error tolerance threshold. After this convergence, the final estimates of voltage magnitudes and angles are used to calculate the total real and reactive power generated, consumed, and lost in the network.

2.1.1.2 Modified Resource Flow Methodology

In order to modify the traditional load flow analysis method, the force and flux have to be identified for a system, proxied as voltage and current, and the resource node supply and consumer node demand have to be specified. The known variables thus become the voltage, or force, at the resources, and the current, or flow demand, at the consumer nodes, called agents. The equations are equivalent to the ones from the traditional load flow method above, since both are based on Kirchhoff's and Ohm's laws, and the underlying thermodynamic laws. As the generalised resource flow is assumed to be directed, however, the modified equations are updated to remove aspects associated with reactive power, and the equations changed to solve for voltage and current, such that power can be calculated after convergence, rather than solving for voltage angle and phase, and calculating power while solving the system of equations.

In RADE networks, the voltages represent the force at which the resources and agents operate. Specifically, at the resources this denotes the potential at which energy is produced prior to being transported through the network to the agents, for example water pressure, electrochemical potential, or the calorific value of food. The voltage at the agents must therefore be lower than that at the resources, as resource flows move down potential gradients, as will be discussed in depth later. The size of this voltage gradient between the resources and agents is co-determined by the resource flow and the resistance along the links, as shown in Eq. (2). In the modified resource flow methodology, current is used to proxy this resource flow, and represents the flow of the energy type that is produced by the resources, such as water, charged ions, or food, of which each agent in the system has a set demand, such as litres or calories per day. The agent voltage then represents its operating potential, or how much useful work or power it can generate with this current flow. Finally, the resistance along the links of the network is therefore the ‘friction’ encountered by this flow as it is moved through the network, incurring energetic losses in the form of heat production, or entropy. In RADE networks, these losses could take the form of water pressure losses due to friction in pipes, or energy losses through heat production caused by the metabolism of organisms, as they expend energy in order to overcome the resistance of the environments through which they move while hunting or foraging (McCrae, 2006). Based on the known potential at each resource, and the known resource flow demand at each agent, the power, or effective operating state at each agent and resource, can be calculated.

In the modified resource flow methodology, first the values in the admittance matrix, from Equation (3) are replaced with those for conductance, the inverse of resistance, or equivalently, the ease with which a steady flow of directed current can pass through a line:

$$G = \frac{1}{R} . \quad (6)$$

To solve for the unknowns, which in this case are the current drawn from each resource node, and the voltage of each agent node, initial estimates are made for each, and the values for the flow of current at each agent based on these estimates are calculated using a modification of Equation (2) in place of Equation (4a). This equation takes into account both the flows of current into the agent, and the flows of current through the

agents to other nodes, but only includes the former terminal flows in the demand consumption calculation:

$$I_i = \sum_{k=1}^N G_{ik} \Delta V_{ik} , \quad (7)$$

where G_{ik} is the conductance between nodes i and k , as calculated in Eq. (6) above, and ΔV_{ik} is the voltage difference between the nodes. As the flow is taken to be analogous to directed current without associated phase angle, voltage is always a simple magnitude in these equations. As this sum is across all in-links, not just the shortest path to a single resource, or paths directly from a resource to agent, it accounts for both direct and indirect flows of current, hence meeting the criterion of including indirect resource flows introduced previously.

The mismatch between calculated and demanded current is determined for each agent, and the updated voltages for each node is calculated using the modified Jacobian, in this case a matrix of partial derivatives of current with respect to voltage, rather than power with respect to voltage as above. As this partial derivative is equal to the inverse of resistance, which is conductance, the conductance matrix constructed previously (Eq. 6) can be reused to solve the system of equations as follows, modified from Eq. (5):

$$[\Delta V] = -J^{-1} [\Delta I] \quad , \quad J = \left[\frac{\partial I}{\partial V} \right] \quad , \quad \frac{\partial I}{\partial V} = R^{-1} = G . \quad (8)$$

The current at each agent is then recalculated using the updated voltages. Unlike the traditional Newton-Raphson method, which requires repeated iterations to converge on a solution due to the nonlinearities of AC power flow, the linearity of the equations for direct current in the modified version allow for it to be solved in a single iteration, as is the case in nodal analysis (Paul, 2001). After the correct current and voltage are determined for each node in this way, the power generated by the resources, used by the agents, and lost due to resistance, and therefore the overall system efficiency, can all be calculated.

2.1.2 Trial runs

In order to test the modified resource flow methodology, four stylised configurations of resources and agents were developed, with the current demand specified at the agents,

and the voltage specified at the resources (Fig. 1). The resistance of the links was set at 1Ω per unit distance. The four configurations represented each combination of one or many agents and resources. These parameters were not reflective of a specific system, but rather were used to test the conservation of flow and the realism of the size-related voltage drops, ergo power losses, within the networks. In each solved network, the total current produced by the resources was equal to the total current demanded, and hence consumed, at the agents, with the current along each link proportional to the voltage difference between nodes at each end of the link, and equal to the product of this difference and the resistance of the link. This shows that the modified resource flow methodology is capable of solving the voltages and currents in both simple and complex networks in a way that is conserving of resource flow and representative of spatially-driven energetic costs. It can thus be applied to analyse both generalised and domain-specific RADE networks, for which analogues of voltage, current, and resistance can be identified.

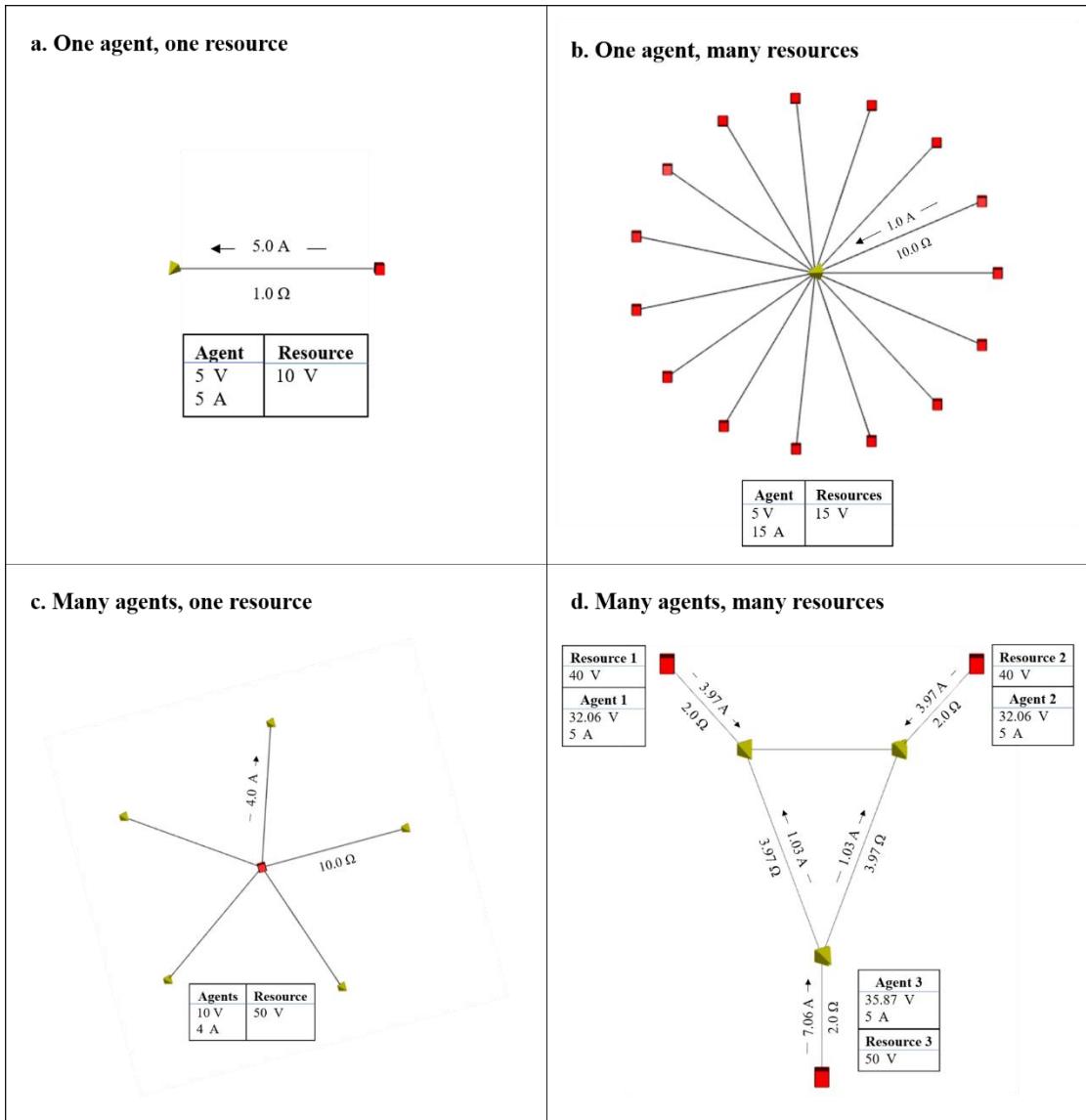


Figure 1. Test networks solved by the modified resource flow methodology. The red squares represent resource supply points, and the yellow tetrahedrons are consumer nodes, or agents. The current demand at agents and current flow along each link (in amps, A), voltage supply at resources (in volts, V), and link resistance (in ohms, Ω), are equal for the agents, resources, and links within the same network, unless specified. The arrows show the direction of current flow, from points of higher to lower voltage.

2.2 Genetic Algorithms

2.2.1 Introduction and Rationale

As previously introduced, both ecological and socio-ecological systems are under selective pressure to maximise their consumption of free energy, while minimising the associated energetic costs with its acquisition and distribution. RADE networks of each can therefore be considered to be progressing toward an optimal state. To replicate that phenomenon in the model here, the generalised, flow-conserving RADE networks developed using the methodology above were optimised using a genetic algorithm (GA). GAs are a subset of evolutionary algorithms, which work by evaluating a population of possible solutions, or ‘chromosomes,’ for their ability at solving a given optimisation problem (Holland, 1975; Goldberg, 1989). The best chromosomes are then used to create the next generation of the population, via so-called genetic operators: computer functions that mimic recombination and mutation. In this way, GAs use Darwinian principles to search for global optima, by improving the population of solutions over time via selective pressure, with the best solutions more likely to propagate their characteristics, or genes, to the next generation.

GAs have been and are still widely used for similar applications in modelling and optimising spatial networks in engineering problems (e.g. Savic & Walters, 1997; Montesinos et. al., 1999; Bakirtzis et. al., 2002; Gen et. al., 2008; Tomoiagă et. al., 2013), optimising parameterisation of spatial models (Polhill & Gimona, 2014), and for some analysis of social networks (Hajeer et. al., 2012), but this work represents one of the first attempts at using them to generate and optimise explicitly spatial networks in ecological and socio-ecological systems, with the end goal of analysing the dynamics and characteristics of those networks. GAs are well-suited for problems necessitating a global search strategy over a high-dimensionality solution space, with the possibility of combinatorial explosion (Klamt & Stelling, 2002), such as the network optimisation done here. They are also highly customisable and can handle optimisations with one or multiple criteria.

Although GAs are powerful optimisers, they are not without their limitations. A common misconception, especially when applied to biological or ecological modelling, is that their evolutionary metaphor, and use of genetic analogues, means that they

accurately portray the process of natural selection via evolution (Hamblin, 2013). GAs are not a faithful replica of the *process* of this type of natural selection-driven development, however, even if and when the results accurately portray natural systems. For this reason, they should be treated as an optimisation tool only, with intermediate phases in the optimisation not necessarily representing intermediate phases of development as would occur in natural systems. For example, intermediate stages of network optimisation could produce structures that real networks would not evolve toward, even temporarily. Other optimisers, namely genetic programming (Koza, 1994), are better suited for optimising processes, via evolving programs and rules. The work presented here was not attempting to model optimal RADE networks by recreating the process of natural selection and incremental construction as applied to them, however. Instead, the aim was to recreate its outcomes via a more general optimisation process, which preferentially selected for and evolved toward outcomes shown to be favourable in ecological and socio-ecological systems.

Another potential pitfall of the GA is that it works by optimising at the systems level, as opposed to the level of individual components. This allows for the modelling of systems-level phenomena, but makes it more difficult to determine the specific role of individuals in the overall pattern. Individual- or agent-based modelling is a popular tool for analysing the latter (Gilbert, 2008), and future work combining it with a GA for RADE network analysis could prove instructive. The argued optimality of distribution networks presented previously occurs at a system-wide level, however, whether that system is the body of an organism (West et. al., 1997) or the global primary energy distribution network (Jarvis et. al., 2015), so optimising the whole network, as opposed to each link or node individually, is accurate.

Finally, one of the most commonly cited arguments against GAs in the technical literature is the number of parameters they require, and the difficulty of identifying the best combination of parameters (De Jong, 1975). Although GAs are quite robust to different parameterisations of some parts of the algorithm (Xu et. al., 2009; Pinel et. al., 2012; Hamblin, 2013), they are extremely sensitive to the specification of the criteria to be optimised, and how that criteria are calculated, as this drives the direction of the optimisation as a whole (Goldberg, 1989). As such, they can prove difficult to program when the exact optimisation criteria are not known *a priori*. While testing different

combinations or specifications of criteria is time- and resource-intensive, it is often the only method to determine this aspect of customisation when it is not explicitly known beforehand. For many optimisations in engineering and mathematics, the exact criteria are known, such as the minimisation of total cost or travel distance, or a maximisation of a mathematical function, and the calculation of that criteria are relatively straightforward. In RADE network optimisation, however, depending on the network in question, it can be more difficult to determine what the ‘costs’ are that the system is trying to minimise. To overcome this limitation, four cost functions are tested and discussed in the proof-of-concept outlined in Section 3.2.3.

2.2.2 Code Flow

The algorithm begins by setting all necessary parameters of functions and creating an initial population of chromosomes. This can be a seed population of known viable solutions, or a random population, as in the network optimisation presented here, called NetGA. These chromosomes are representations of possible solutions, typically encoded as bit strings (Goldberg, 1989), or as customised data structures. The different parts of the encoding, which are altered by the algorithm over the course of the optimisation, are called ‘genes.’ In NetGA, the chromosome (Fig. 2), is a customised data structure representing the network, which holds the locations of agents and resources, which are fixed, and the evolvable genes: locations of mobile branch points, which are non-demand junctions between links that allow the GA to explore different network configurations; the resource flow demand for the agents, proxied as current; and the matrix of connections between all the nodes in the network.

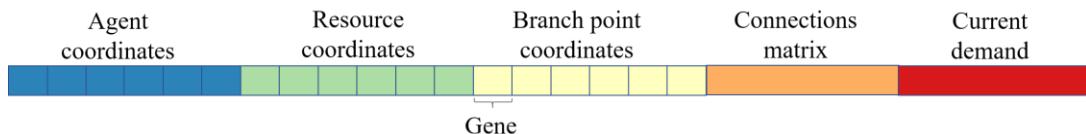


Figure 2. Network chromosome. A chromosome in a GA represents a single solution to the optimisation problem: in this case, a network, with the coordinates of resource-consuming agent nodes, resource supply nodes, and branch points allowing for exploration of different network structures, as well as the matrix of connections between each of these nodes, and the demand of current, a proxy for resource flow. Each of these individual components is called a ‘gene’.

After initialisation, the algorithm executes its main loop (Fig. 3), which consists of iteratively evaluating and improving the solutions, until a specified termination criterion is met. The evaluation portion of the algorithm is known as the cost function, if the criteria for optimisation are meant to be minimised, or the fitness function, if maximised. In this function, the algorithm evaluates each chromosome for its ability to minimise or maximise each criterion. For conciseness, cost/fitness functions are referred to hereon as cost functions, regardless of the goals of optimisation. Details of the cost functions tested in the proof of concept for NetGA are discussed in Section 3.2.3.

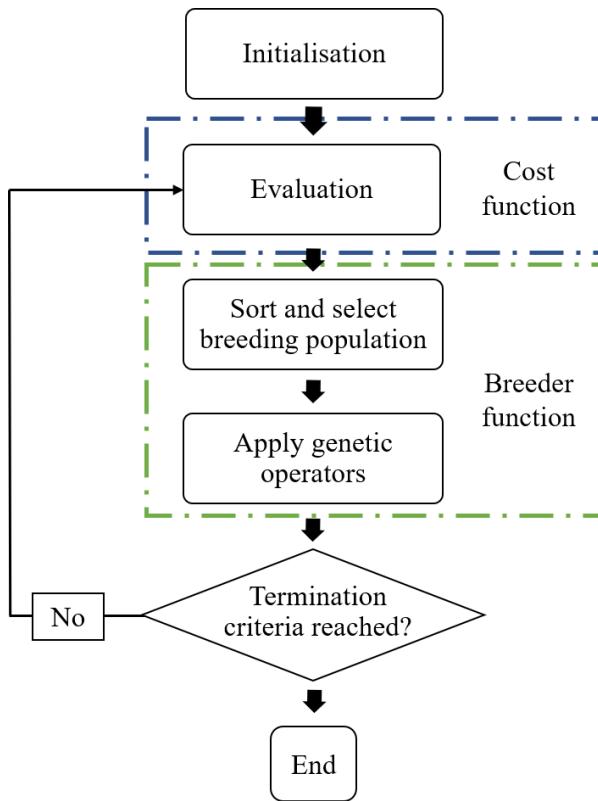


Figure 3. Code flow of a genetic algorithm. After initialisation, the main loop involves iteratively evaluating and producing new generations of solutions. After each generation is produced, the algorithm tests whether it has reached pre-specified termination criteria. If so, it ends the optimisation and reports the best solution(s) found, otherwise it continues repeating the main loop. The evaluation is done in the cost function, while the ranking of the population by performance, selection of best individuals, and application of genetic operators to produce the next generation all occur in the breeder function.

Following this evaluation, the population is then ranked by cost, and the next generation created or bred from a selected subset of the current population, the breeding population, by applying so-called ‘genetic operators,’ or functions designed to imitate genetic recombination and mutation. In NetGA, ranking is done based on population-normalised performance on each of the criterion in the cost function. If there is more than one criterion in the cost function, the ranking is determined by how many networks a given solution is Pareto-dominated by, with Pareto-domination defined as one network performing equally or better on each criterion than the compared network (Fonseca & Fleming, 1993). If a network performs better on some criteria but worse on others than the compared network, the two networks are incomparable. This comparability can be conceptualised most easily for a two- or three-criteria cost function as there being a positive gradient between the two networks when the solution trade-off space is plotted using Cartesian coordinates (Fig. 4). The fewer networks that a given network is dominated by, the higher it is in the ranking. Ties are broken in ranking by how many networks a given network dominates, with the more dominating networks ranked higher. If there was only one criterion in the cost function, then ranking is simply an ordering based on performance on that criterion.

The highest-ranked networks from each generation are then automatically added to the next generation, an optimisation strategy known as elitism (De Jong, 1975), and the lowest-ranked networks are removed from the current population, known as truncation, before being replaced with a copy of the best networks (Montesinos et. al., 1999). For multi-criteria cost functions, the population is further pruned by dividing it into niches of a set capacity (Horn et. al., 1994), with each niche comprised of networks within a certain threshold similarity of performance on all of the cost criteria. Additional networks beyond the capacity of the appropriate niche are removed from the population (Pétrrowski, 1996), encouraging diversity across the Pareto front and avoiding premature convergence on local optima.

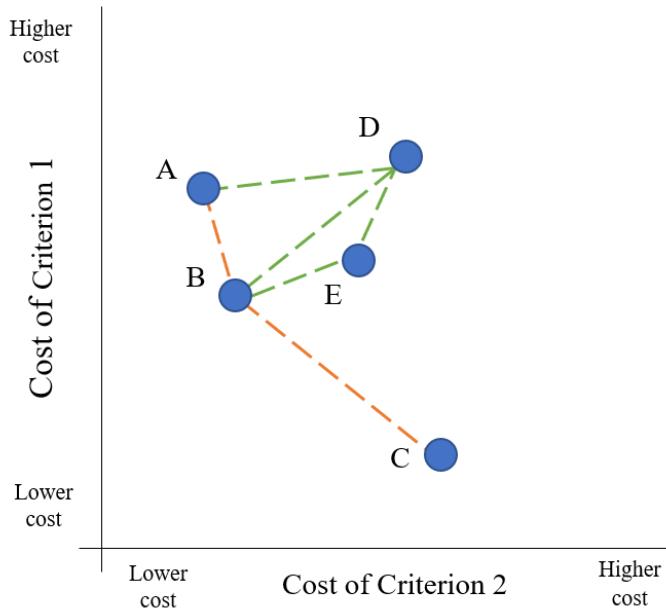


Figure 4. Pareto dominance, shown for a two-criteria cost function. In this example, the blue circles represent solutions, such as network chromosomes in NetGA, plotted according to their performance on each criterion, with lower cost being preferable. Solutions A, B, and C are all incomparable, as there is a negative gradient between them. These solutions make up the non-dominated Pareto front, as there are no solutions that perform better than them. Solutions E and D are both dominated by B, and D is dominated by A. As B dominates two solutions, and A one, B would be placed higher in the ranking, such that the final ranking of these five networks would be B, A, C, E, D. Other incomparable dominance links between A and E, C and D, and C and E, are omitted for clarity.

In GAs, selection is typically done in one of three ways: via tournament, where the chromosomes are compared in a pairwise manner, with the less costly of the two chosen as the winner; truncation, where a set number of chromosomes are eliminated before breeding; or through fitness-proportionate selection, where the probability of a chromosome being selected for breeding is proportional to its fitness, or inverse cost, relative to the total fitness of the population (Goldberg & Deb, 1991). Within fitness-proportionate selection, there is roulette-wheel selection (Fig. 5a), which generates a cumulative probability distribution of population fitness and selects individuals from it randomly (Goldberg, 1989), and stochastic universal sampling (Fig. 5b), utilised in NetGA, which samples the cumulative probability distribution at evenly spaced intervals (Baker, 1987). The latter is considered a superior implementation, as it is less likely to be biased to only select members of the population with comparatively high fitness. Preserving some of the genetic material, or solution characteristics, of poorer performing solutions is necessary for encouraging global search and not allowing the algorithm to converge prematurely on local optima. It is often the combination of some of these genes with those of other solutions that allow the GA to find the global optima.

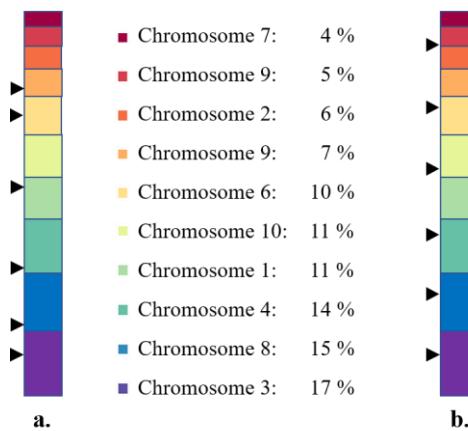


Figure 5. Fitness proportionate selection methods applied to a population of ten chromosomes of varying fitness. The size of the block reflects the fitness of the chromosome, or its performance on the given optimisation problem, as a percentage of the total population fitness. The percentage is also shown for each chromosome. **a.** Roulette wheel selection of six pointers (black triangles). Pointer placement is done via repeated random sample, which can be with or without replacement. **b.** Stochastic universal sampling of same population, which samples at evenly-spaced intervals across the cumulative probability distribution of fitness for the population.

During crossover in NetGA, two networks are chosen as parents from the breeding population. The genes of each network are exchanged uniformly such that each offspring receives a given gene with equal probability from each parent (Fig. 6a) (De Jong & Spears, 1992). This is in contrast to single- and multi-point crossover (Fig. 6b and c), which are less disruptive of the solution, but also provide less coverage of the solution space.

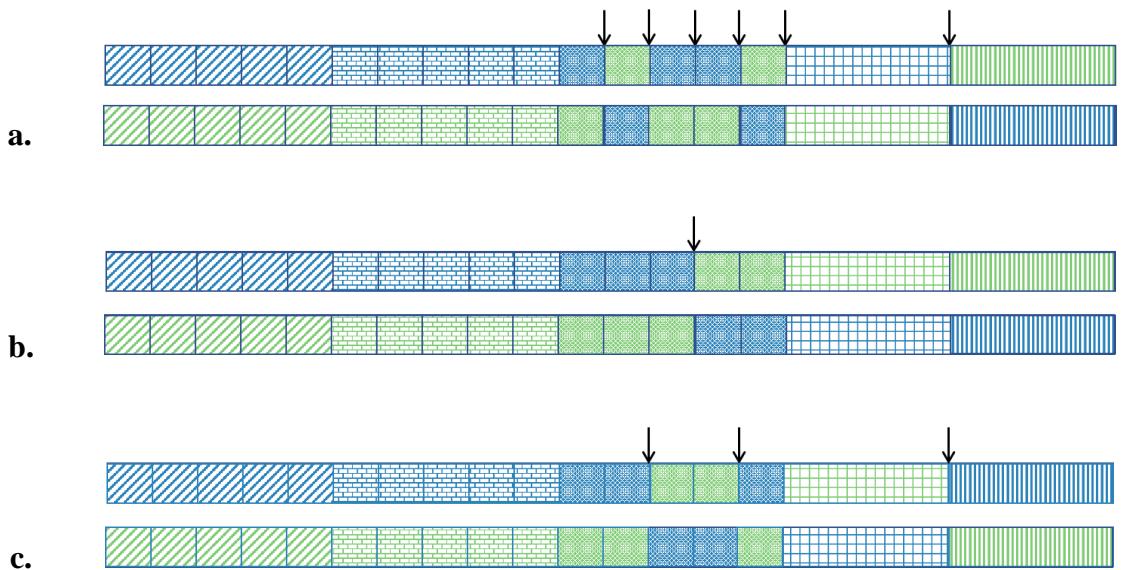


Figure 6. Variations of crossover operations. The two bars are the two offspring solutions, represented here using network chromosomes (Fig. 2), resulting from a crossover operation, where two parent chromosomes are recombined. The shading denotes the different types of genes encoding the parts of the network, and the colour represents from which parent network the genes originated. Note that the first two blocks of genes, agent and resource locations, are the same for all members of the population and fixed for the duration of the optimisation, so are not exchanged. The black arrows indicate the crossover points. **a.** Uniform crossover, where the offspring chromosomes receive the genetic material from one parent or the other with equal likelihood at each gene, such that on average, each offspring is made up of half of each parents' genetic material. **b.** Single-point crossover (not used in NetGA), where each offspring receives the genetic material from one parent for a portion of their chromosome, and the material from the other parent for the other portion. **c.** Multi-point crossover (not used in NetGA), where each offspring receives multiple portions of genetic material from each parent.

After crossover, each offspring undergoes perturbation with a certain probability (Fig. 7). In perturbation, each branch point location, the strength or weight of each connection, and the current demand for the agents, is altered to a new value within a given variance from its current value, with each alteration happening with the same overall perturbation probability. Perturbation is not a genetic operator typical to GAs but is useful for exploring the local neighbourhood of the solution space around the results of the crossover, by acting as a hill-climbing operator without disrupting too much of the solution. If the new networks are not created through crossover and perturbation, the parent networks are cloned, and each of the clones undergoes mutation, where each gene is mutated with a certain probability, to a new value drawn from a uniform distribution within the permitted range (Goldberg, 1989). This process of crossover and perturbation, or mutation, is repeated to fill the next generation of the population.

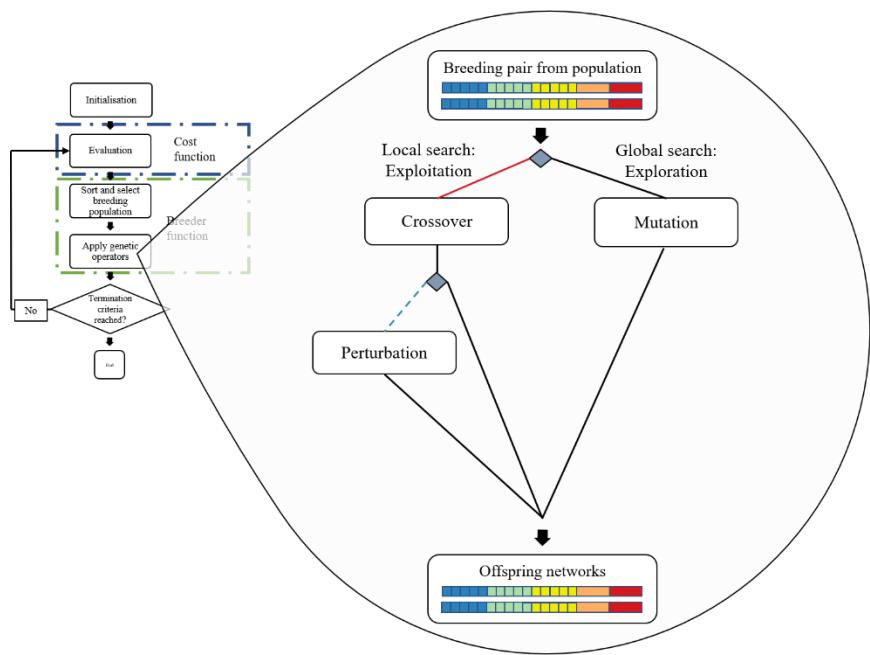


Figure 7. Genetic operator code flow. The inset represents the flow of operators occurring within the breeder function, as located within the overall code flow on the left (see Fig. 3). The diamonds represent decision points, with the red line showing increased probability of crossover-generated networks, and the blue dashed lines showing the decreased probabilities of perturbation after crossover. The specific values of these parameters, and the increasing or annealing schedule of each, is different for each optimisation, depending on the complexity of the problem.

Although many GAs perform both crossover and mutation to generate each new solution, here the two operators are separated based on their effect. While crossover and perturbation operate more as local search operators to exploit promising areas in the solution space (Srinivas & Patnaik, 1994; Smith & Fogarty, 1997), mutation acts as a global search operator, to explore new areas of the solution space throughout the optimisation, and to avoid premature convergence. Over the course of the optimisation, the overall probability of new network generation via crossover and perturbation increases, which effectively also decreases the probability of mutation of an entire network, and the probability of perturbation for these crossover-generated networks decreases. This selective annealing of some probabilities and increasing of others encourages a wider exploration of the solution space initially, when the performance of each network is poorer across the three criteria, and allows the optimisation to explore the possibility of improved performance by combining the qualities of high-performing networks later in the optimisation, reducing the likelihood and amount that good solutions are disrupted.

The process of evaluating and generating new populations of network chromosomes is repeated until set termination criteria are reached, at which point the best network, for single criterion cost functions, or Pareto front of networks, for multi-criteria cost functions, are returned. In NetGA, this termination criterion is a pre-specified number of generations, determined through testing different values and choosing one that is long enough to allow for convergence, while remaining within a reasonable runtime, as discussed in Section 3.2.4. An alternative criterion utilised in some GAs is a threshold number of generations during which significant change is not seen in the best ranked solution(s) (Safe et. al., 2004), but thresholds for both the number of generations and the significance of change are difficult to quantify, which can lead to premature termination if the GA were to settle temporarily on a local optimum. Specifying a high number of total generations as the termination criterion allows the GA to fully explore the solution space, and keeping the best network(s) found in each generation ensures that the historical optimum achieved will not be lost at any point of the optimisation.

3. Test Case: Nectar Foraging Networks of the European Honey Bee, *Apis mellifera*

3.1 Rationale

In order to test the ability of NetGA to model real-world RADE networks, a proof-of-concept was developed around the nectar foraging networks of the European honey bee, *Apis mellifera*. *A. mellifera* is the most widespread honey bee species, found on every continent except Antarctica, mostly as a result of human transportation and introduction efforts (Meixner, 2010). Their role as pollinators makes them vital to ecological and socio-ecological systems, through maintaining and facilitating plant biodiversity, ecosystem stability, agricultural production, and food security (Potts et. al., 2010). For this reason, they are widely studied, providing a solid dataset with which to parameterise the GA and qualitatively evaluate the resulting optimised networks. Furthermore, they are known central-place foragers (Kacelnik et. al., 1986), gathering nectar from distributed sources but always returning directly to the hive, which led to a simple, constrained proof-of-concept, representing the hive as a single, fixed-location point of resource demand, and the floral resources as fixed-location points of resource supply.

Studying nectar foraging networks in this way was also an interesting test case in its own right, as it modelled a distributed network from a whole-systems perspective. A colony of honey bees has been compared to a ‘superorganism,’ utilising the information gathering and sharing activities of each forager bee to orchestrate a highly coordinated yet entirely decentralised foraging effort (Gillooly et. al., 2010). This allows the colony as a whole to operate as effectively as if each bee had complete information about all nectar sources available (Seeley, 1995), which justifies modelling the foraging dynamics as optimal at a colony level, as opposed to the level of an individual forager. Further research on the explicitly spatial aspect of colony-wide nectar foraging efforts would allow for a better understanding of the energetic costs of foraging in different spatial distributions of resources, and therefore more accurate calculation of land-use impact on nectar foraging and pollination (Becher et. al., 2014). Similar optimisation could also be applied to the placement of hives in commercial bee-keeping set-ups, which has only been studied to a limited extent with mathematical programming (Esteves et. al., 2010; Tamboan et. al., 2011; Gavina et. al., 2014), and could facilitate

greater pollination coverage, prediction of honey quality and composition, and improved colony health through access to a diversity of pollen and nectar nutrients.

3.2 Parameterisation

The parameters used for the modelling and optimisation of any type of network using NetGA are those required for construction of the topology filled by the network, construction of the population of networks for each generation, and the design and parameters of the breeder and cost functions to fit the specific optimisation criteria. For the nectar foraging network optimisation, called HiveNetGA, this was done to approximate known foraging conditions and dynamics of *A. mellifera* as reported in the literature. While the overall code flow of NetGA was maintained, the specific parameterisation guided HiveNetGA to optimise networks consistent with the approximate conditions and theorised constraints of nectar foraging networks. This parameterisation was not meant to be an exact replica of the foraging conditions experienced by *A. mellifera*, as those are highly heterogenous for each colony, depending on its geographic location and the time of year, and even the time of day, as flowers vary considerably in nectar production and sugar concentration over the course of a twenty-four-hour period (Adgaba et. al., 2017). Instead, the parameterisation was a realistic, data-driven approximation, for the purposes of developing and testing the generalised model of spatially-explicit RADE networks. Similar approximations have been used in other models of foraging patterns (e.g. Wallis DeVries, 1996; Ward et. al., 2000; Baveco et. al., 2016), when it is the overall dynamics of the system in question, as opposed to the realism of input parameters, that is being tested (Levins, 1966).

3.2.1 Topology

To design the overall environment for the nectar foraging networks, the topology parameterisation required identifying a reasonable analogue for nectar resource ‘voltage’ and bee colony ‘current’ demand for use in the modified resource flow calculations, and creating distribution maps of the resources that were realistic enough to approximate honey bee foraging habitats.

As discussed earlier, current is a measure of the rate of flow of charged particles, measured in amps (coulombs sec⁻¹) in electrical networks, and represents the flow of

the energy type that is produced by the resources, of which the consumers in the system have a set demand. The analogous element in nectar foraging networks would therefore be the rate of flow of nectar from flowers back to the hive, as carried by the forager bees. Calculations of average colony foraging efforts (from Harrison & Fewell (2002), unless otherwise noted) were used to derive a realistic approximation of this nectar flow to the hive:

Table 1. Calculations of nectar in-flow to a mature hive.

Size of mature colony	30000 bees (Seeley, 1995)
Percent of colony that forages	15 %
Nectar load of a single forager	30 mg
Number of foraging trips	10 trips/forager/day
Total nectar delivery to hive (calculated)	15.625 mg sec ⁻¹

Similarly, the analogue for voltage in these foraging networks would be the energetic potential, or charge, of the nectar itself, which can be measured as the nectar sugar concentration. While bees require both pollen and nectar, the former is mostly a source of protein (Donkersley et. al., 2014), while the latter provides the essential carbohydrates for the foraging, nestmaking, and brood-rearing activities of a colony (Seeley, 1995), hence it is the energy resource in focus here. Honey bees prefer nectar sugar concentrations close to 50 % (Seeley, 1995), but the nectar from the flowers and trees from which they gather varies in sugar concentration across and even within species, for different seasons and times of day. Although temporal variation was not considered within this simulation, as each optimised network represented a fixed moment in time, the heterogeneity of nectar resources was represented by modelling the resource points as different species frequented by *A. mellifera*, with each species having a unique level of sugar concentration reflective of the average for that species. The ‘voltage’, then, at each resource point was calculated as:

$$V = uC \quad (9)$$

where u is 17.2 J mg⁻¹, the energetic value of sugar in nectar (Seeley, 1989), and C is the nectar sugar concentration of that species, in mg mg⁻¹, so that V is measured in J mg⁻¹. The nectar flow to the hive above was calculated in mg sec⁻¹ averaged over the

course of a 24-hour period, so that the final energy transfer measure at the hive would be consistent with the SI unit for power (W, or J sec⁻¹).

Along with the voltage and current, the analogous element for resistance in the foraging networks had to be identified. As the networks are made up of forager flight paths, the resistive losses are due to distance travelled, as this increases the foragers' energy expenditure in transporting the nectar. In order to simplify the proof of concept presented here, variability in losses due to effects of weather conditions, such as wind drag and temperature, were assumed to be equal per unit length, such that the resistance was calculated as simply the length of the links between the resources and hive.

As introduced previously, the energetic losses caused by flow along these resistive links determine the gradient between the voltage at the resources and hive (Fig. 8a). It would seem that the hive, with its 20 kg of nectar stored in the form of honey for consumption over the winter, and another 70 kg of nectar consumed over the summer to provide food for foraging, nestmaking, and brood-rearing (Seeley, 1995), would be of considerably higher 'potential' than the delicate flowers from where the bees collect nectar. Instead, however, it can be conceptualised as operating at a lower potential, due to the expenditure of energy in overcoming the energetic costs of nectar transportation efforts, as the foragers refuel with stored nectar before beginning their next journey (Seeley, 1995). In the modified resource flow methodology, the voltage drop acts as a proxy for the consumption of some of the previously-gathered energy, to allow for the transportation of new resource flows (Fig. 8b). This is akin to the process of active transport across cell membranes, when the coupling of energy flows allows for molecules to move up concentration gradients (Lodish et. al., 2000): this seemingly 'upgradient' process is actually downgradient, as with all energetic flows, when system boundaries are drawn appropriately in time and space to include all relevant energy flows into the process under study. In the case of foraging networks, the upgradient paradox is resolved by increasing the timescale slightly to include the exchange of nectar at the hive between foragers and hive bees, as the former both deposit and receive energy flows.

After fuelling foraging, the remainder of these flows are invested in infrastructure (Fig. 8c), defined here to mean the embodiment of energy in materials (Jarvis, 2018). In the foraging networks, this infrastructure is in the form of honey, forager bees, and the hive

itself, representing long-term energy stores, and energy collection and storage infrastructures, respectively. In contrast with the short-term energy storage of nectar, which is almost immediately remobilised as a flow of energy for another forager or hive bee, the energy embodied in infrastructure can only be remobilised through decay. Both the process of remobilising flows to be expended in future foraging efforts, and the embodiment of energy in infrastructure are energy transformations or phase changes that occur primarily in time, as opposed to the predominately spatial phase change that occurs when the energy flows are brought back to the hive (Fig. 8a).

The expenditure of energy through foraging and as embodied in infrastructure can thus both be conceptualised as energy ‘sinks,’ even though they are not losses per se. As the final infrastructure creation and decay process is not modelled here, however, the voltage at the hive measured by the resource flow methodology is a combination of that which is used for infrastructure creation and lost through decay.

$$\text{Energy throughflow of whole system: } P_T = \sum I_N V_N = P_C + P_F$$

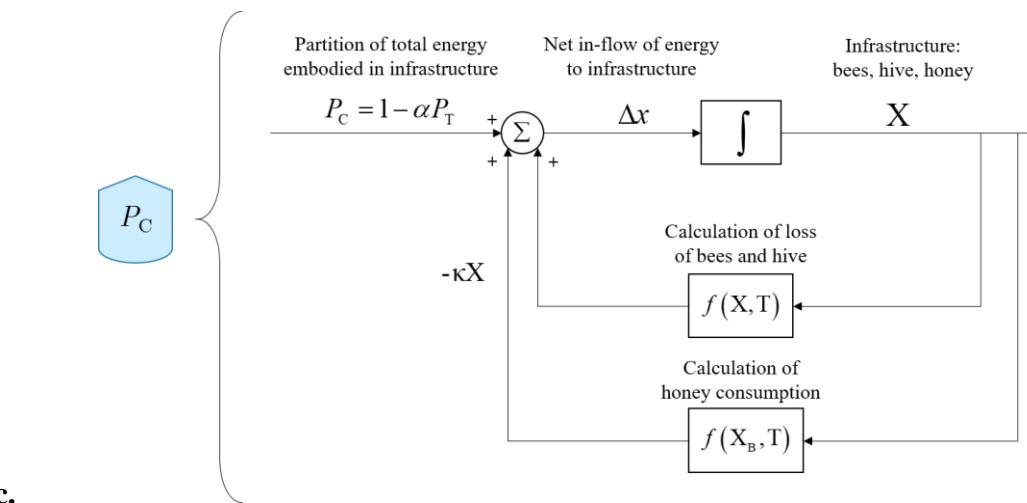
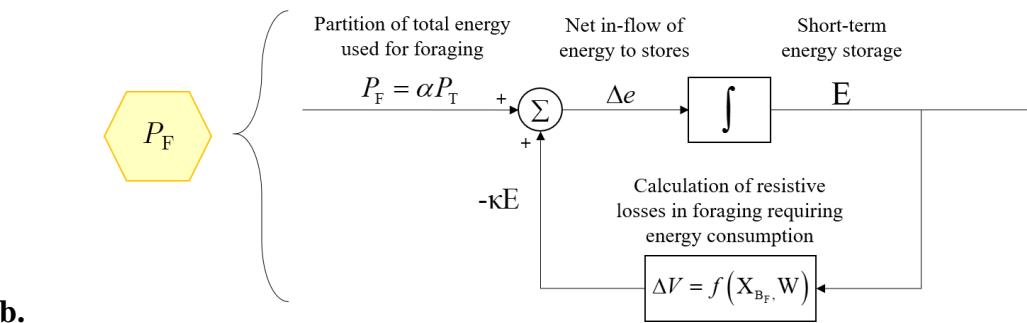
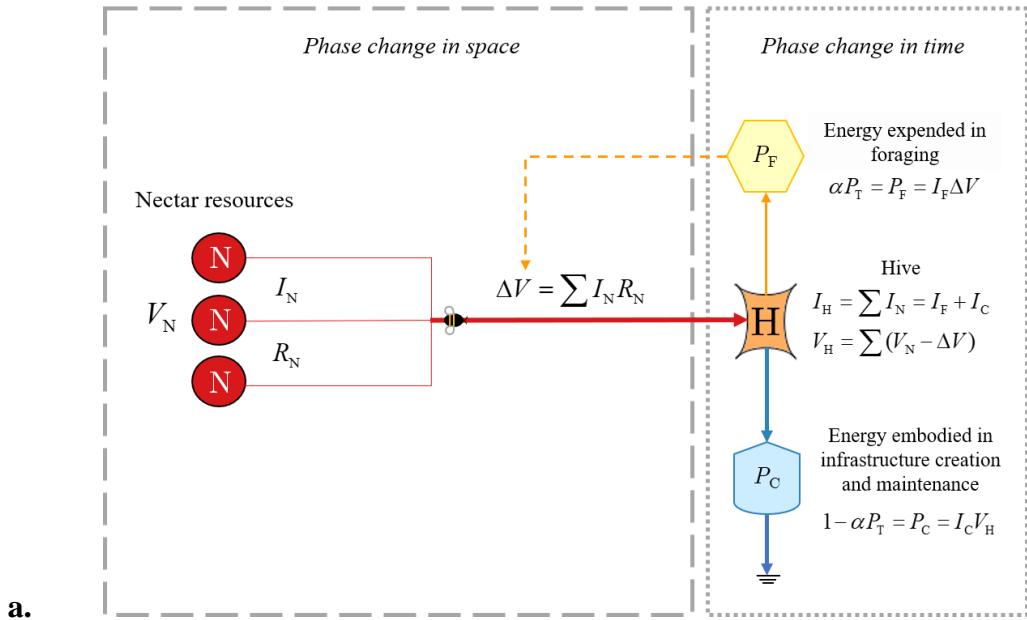


Figure 8. Energy flow in nectar foraging networks. **a.** The voltage (V), current (I), resistance (R), and power (P) are represented for the different elements of a nectar foraging network. The flow of nectar energy into the hive is partitioned into energy that will be expended in foraging (P_F), and energy that will be embodied in infrastructure creation and maintenance (P_C). The phase changes denote energy transformations, across space from resources to hive, and across time in the partitioning between energy used in foraging or embodied in infrastructure. Note that current, I , is conserved through the network, representing the conservation of resource flow. **b.** The flow of energy expended in foraging. The energy into the system, P_F , is the total energy into the hive, times a partitioning coefficient, α , which determines how much energy of the total inflow is used for foraging. In bees, this is approximately 30 % (Harrison and Fewell, 2002). This in-flow is offset by the decay rate of the current stock of energy, $-\kappa E$, which represents energy used to offset the resistive losses experienced by foragers, i.e. their metabolism, which is a function of the number of bees that are foragers, and the weather conditions that affect their flights and the nectar flows. These are combined and proxied by voltage drop in the networks modelled by the modified resource flow methodology. The net in-flow after this consumption, Δe , is then transformed into the total stock of short-term energy stores, E . **c.** The flow of energy embodied in infrastructure, which is the total energy minus the partition used for foraging. The net flow of energy into infrastructure, $\Delta \chi$, is the total flow minus losses due to decay of long-term energy stores over the winter, and death and damage to physical infrastructure: the bees and hive. The total stock of infrastructure is represented by X . The physical infrastructure decay is a function of the current stock of infrastructure, and the season, as bee lifespans and hive decay are both affected by the season (Seeley, 1995). The long-term energy stores decay, or honey loss, is a function of the total bees consuming it, and the temperature, as this decay happens almost exclusively during winter when it is too cold for plants to produce nectar. The symbols used for consumption (P_F), storage (P_C), switch (H), and source (N) are adapted from the ‘Energy Systems Language’, developed by H.T. Odum (1971, 1983).

In order to generate realistic resource distributions for the genetic algorithm to explore in network optimisation, a dataset for UK floral abundance was used, which quantified the frequency and distributions of common British plant species for a range of habitat types in the greater Bristol area, as part of a study linking land use change and pollinator population health indicators (Baude et. al., 2015). The nectar sugar concentration was identified for 25 of these species across different habitats, using the nectar sugar concentration of a closely related species if data was not available for the exact species in question, and the voltage at each nectar resource was calculated using Equation (9) above.

The selected resources were then partitioned into five major habitat groups – grassland, grassland farmland, grassland park, grassland woodland, and woodland, and the percentage of vegetative area covered by each species within the given habitat was used to determine how many resource points representing that species to place on the resource distribution map. The locations for each species were plotted based on the area covered by that habitat in each resource map, with each species distributed within its assigned habitat area in the resource map. For example, survey data showed the buttercup, *R. bulbosus*, as occurring in both grassland farmland and grassland park habitats, with a vegetative area covering approximately 0.87 % and 2.04 % of the two habitats, respectively. As such, one was placed in the grassland farmland resource distribution map, and two in the grassland park resource distribution map. A complete listing of the species used in each habitat, their nectar sugar concentration, and the calculated voltage, is included in Appendix A.

The overall spatial topology of each resource distribution map was a three-dimensional plane, with maximum coordinates 28 x 28 x 0.035, and a hive placed relatively centrally, with fixed coordinates for resources and hive throughout the duration of the optimisation. This sizing was chosen as bees have been shown to typically forage within a 784 km² area around the hive, and most foraging flights are within 6 km (Seeley, 1995). The heights of the resources and of the hive were taken into account in their distribution, with tree species represented as 2 – 3.5 m in height, and flower and shrub species as 0 – 1 m in height.

3.2.2 Network Construction

As in the general NetGA, the network chromosome in HiveNetGA also contained the coordinates of branch points, the non-demand junctions between links. HiveNetGA could disconnect branch points or move them directly beneath the hive to shorten their link length to functionally zero. Therefore, it was not constrained by using them, and they did not influence power consumption beyond their impact on link length. As bees have been shown to navigate by using landmarks (Menzel et. al., 2005), inclusion of these branch points allows for possible representation of this in the resulting network structure. Five branch points were included in each network chromosome, as this number allowed for potential exploration of meaningfully different structures within the spatial topology provided, without considerably adding to the computational burden of a larger possible solution space. During initialisation, the branch points were placed randomly at points drawn from a uniform distribution bounded by the maximum coordinates of the topology.

The final element of the network chromosome was the matrix of connections between the different nodes that comprised the network: resources, branch points, and the hive. In some optimisations, link strength, such as the width of a road or pipe, would be included in this matrix to weight the connection appropriately, but link strength was not included in HiveNetGA. The reasons for this were two-fold: Primarily, as the links in a foraging network are simply the flight paths of bees as they traverse the airspace between the nectar resources and hive, it can be argued that these links all have the same carrying capacity, equal to one bee's worth. The amount of current drawn down the link then represents the number of bees traversing it to bring nectar in from the resource it connects back to the hive, such that the 'resistance' of that link, resulting in energy lost in traversing it, is directly proportional to its length, since each bee experiences this resistance approximately equally. Closer resources, which have lower resistance links to them, would naturally be exploited by more bees, replicated here by higher current flow. Secondly, as GAs typically perform best with a limited number of variables to optimise, link strength was excluded to limit the degrees of freedom in this small proof-of-concept. Future work is planned to investigate the effect of link strength in other case studies, but for the purposes herein, the matrix gene was binary: a link either existed between two nodes, or it did not. Nodes were allowed to connect to one another freely, with the exception of resources, which could only connect to the hive or a branch point.

This was designed to approximate the flower-constancy of honey bees, who only gather nectar from one species per foraging trip (Aristotle, cited in Grant, 1950). As the voltage was equal for all nectar resources of a given type, and current only flows down voltage gradients, there would be no flow between resources of the same type, rendering intraspecies connections useless.

During the first round of testing HiveNetGA, the mutation operator in the breeder function could remove links with the probability of one minus the initial connection probability. As such, the initial connection probability was set at 0.9 to keep the rate of disconnection slow. After testing this with the two single criterion optimisations in the first round, as presented in Section 3.4.1, the mutation operator was changed so that it did not disconnect links. Instead, the only way that a network would have more disconnected links than either parent was if it had disconnections from both parents expressed in its connections matrix. This slowed the rate at which HiveNetGA explored disconnected networks, thus increasing the selective pressure to minimise resistance-driven losses by optimising existing links. After changing this, the initial connection probability was decreased to 0.75 for the single criterion cost functions. Initial connection probabilities of both 0.75 and 0.5 were tested for the multi-criteria cost functions, to further assess the behaviour of the algorithm with different levels of connectivity.

3.2.3 Cost functions

As the cost function is the ultimate driver of the optimisation, since it defines the criteria of optimality that each solution is assessed with respect to, its specification is vital to the performance of the GA. In ecological modelling, the costs experienced by a system are sometimes obvious, such as the ubiquitous energetic cost of movement, and by extension, transportation of resources. Other costs, however, may not be so visible or easy to quantify. The prevalence of homeostatic control (Cannon, 1929) and similar mechanisms alleviate some of these complexities, by presenting a more homogenous response at a systems level, but it is still difficult to accurately determine the process or costs incurred by observing the product or end state of the system (Bascompte, 2007). To try to navigate this dilemma in HiveNetGA, four cost functions of varying levels of complexity were tested for the optimisation, and each assessed as to the possible validity of networks produced. These are described in detail below and summarised in Table 2.

It should be noted that although some of these functions were maximising a quantity, and therefore technically fitness functions, the term ‘cost function’ is still used throughout to maintain consistency.

3.2.3.1 Single Criterion Cost Functions

The first cost function, called Maximum Efficiency Cost Function (MECF), attempted to maximise the efficiency of the network, defined as the ratio of power consumed at the hive to power produced at the resources. Power is defined as the product of voltage and current:

$$P = IV \quad (10)$$

As such, the power at a resource point was the nectar sugar concentration, or voltage, at that resource, times the flow, or current, drawn from it, and can be conceptualised as the total energetic input of the resource to the foraging network, as demanded by the hive through connections to the resource. The power at the hive was then the specified nectar flow demand proxied as current, times the voltage at the hive, which was calculated by the modified resource flow methodology based on the resistances of the links between the hive and resources, along which the nectar flow occurs. While models of some species maximise the rate of energy intake while foraging (e.g. Stephens & Krebs, 1986; Ward et. al., 2000), assuming that the individuals attempt to collect the maximum energy per unit of time, honey bees have been shown to attempt to maximise energetic efficiency, as their lifespans are dictated by energy expenditure more than time (Seeley, 1995).

Although a simple, single criterion cost function, attempting to maximise the energetic efficiency of a network should optimise the links so as to lose minimal power due to resistance. As discussed above, resistance is directly proportional to link length in this optimisation, so to minimise resistance-based losses, link length should be minimised. This single cost should then encompass the foragers’ goals of maximising energy gathered per unit of energy expended, by maximising power consumption through minimising power loss.

Along with the proven imperative to maximise energetic efficiency, some sources posit that this is equivalent to maximising overall consumption at the hive, in terms of a

quantity of nectar collected as opposed to a ratio of collection to total afforded by the resources (Seeley, 1995). As a high efficiency simply denotes a high rate of retention of energy flow, regardless of the actual final quantity of energy, it could be argued that the overall colony objective would be to maximise total consumption through maximising individual efficiency. As the optimisation operates at the network level, and was parameterised to represent the foraging of an entire colony as opposed to a single forager, it could be more accurate to attempt to optimise this total quantity of consumption instead of efficiency. As such, another cost function was designed, similar to the one above, called Maximum Power Cost Function (MPCF), which tried to maximise the energy consumption, modelled as power, at the hive. Although subtle, the difference between maximising the efficiency and the consumption of a network proved to have considerable effects on the resulting structure, as presented in the Section 3.4.1.

3.2.3.2 *Multi-criteria Cost Functions*

The third and fourth cost functions tested were multi-criteria, with the additional criteria used to further assess the characteristics of networks produced under selective pressure from multiple, potentially conflicting imperatives; and provide additional insight on network modelling and optimisation with GAs. Although multi-criteria optimisation uses all the criteria to evaluate each possible solution and direct the optimisation, the final solutions are Pareto optimal in that they may be the best performing in one criterion, but not in all criteria. The use of multiple criteria therefore directs and constrains the optimisation as a whole, but the criteria can only constrain one another to a limited extent.

The third cost function, Maximum Power Minimum Links (MPML) incorporated maximising power via MPCF above, while simultaneously minimising total link length. This was designed in response to the characteristics of the networks produced by the single criterion cost functions, presented in Section 3.4.1, which seemed to favour maximising the lengths of some links, in order to minimise the current per link. This can be explained by a simple derivation from the laws presented in Section 2.1.1. By using Ohm's law (Eq. 2) to define the voltage at the hive as the voltage at a resource, minus the product of current and resistance along the links between the hive and the resource, and including the conservation of current as defined by Kirchhoff's current

law (Eq. 1) such that current is conserved between the hive and resources, the power at the hive can be calculated by:

$$P_H = IV_H = I(V_R - IR) = IV_R - I^2R = P_R - I^2R \quad (11)$$

The loss term in this equation, I^2R , is the power lost due to Joule heating between the power at the resource, P_R , and at the hive, P_H . In foraging networks, this represents the heat produced by the forager bees' metabolisms, and the displacement of air molecules as they fly. As the current term in the power loss calculation is squared, the power loss along a link is much more influenced by the quantity of current along that link, than its inherent resistance. In any optimisation based on power loss, therefore, HiveNetGA will attempt to minimise this loss by minimising the link lengths, or resistances, for most of the links, but may also include much longer links to decrease the amount of current flowing down each shorter, lower resistance link. While this phenomenon was displayed more prominently in MECF (Fig. 11a), the criterion to minimise total link length is valid for MPCF as well, as maximising power consumption similarly necessitates minimising loss. As such, this criterion was combined with MPCF, since MPCF was more likely to be accurate in the context of an explicitly system- or colony-level optimisation.

For MPML, the total link length around the network was calculated as the sum of the length l of all links $i = 1..nLinks$ in the network:

$$L_T = \sum_{i=1}^{nLinks} l_i \quad (12)$$

In order to simplify the Pareto dominance calculation in HiveNetGA, as discussed previously for NetGA optimisations in general, MPML attempted to minimise both the inverse of power consumption, and the total link length, as opposed to maximising power consumption and minimising link length. This technique of minimising an inverse quality has been used successfully to simplify other network optimisations (Gandomkar et. al., 2005), especially when they combine multiple criteria, with some criteria to maximise and some to minimise.

The minimisations of inverse power consumption and link length were also included in the fourth and final cost function, Maximum Power Minimum Resource Disconnection (MPMR), which added a third criterion to minimise the number of resource types to

which the hive was not connected, either directly or via a branch point. This constraint was to encourage HiveNetGA to explore networks that attempted to connect to the maximum number of resources, in order to maximise power and minimise disconnected resource types, but in a way that minimised link cost. *A. mellifera* require a diversity of nectar sources, as these provide a range of essential amino acids, as well as carbohydrates (Nicolson, 2011). Furthermore, this gives the colony greater flexibility should a given resource patch become unusable or decrease in nectar yield. As such, it would be logical for a bee-optimal network to favour connecting to a range of resources, even if this somewhat increases the energetic cost of foraging: a necessary trade-off to increase the resilience of the colony.

To calculate the disconnected resources, HiveNetGA used the connections matrix to create a mapping of all first-level, or direct connections between all nodes: resources, branch points, and the hive. These connections were then traversed recursively to build up a list of all indirect connections, defined as nodes that were connected via links to one or more intermediate nodes. When combined, the resulting all-connections matrix thus showed all nodes reachable from a given node. Using this, it could be determined which resources connected directly or indirectly to the hive. If no resource points of a given type were connected to the hive, it was added to the disconnected list, the length of which was used as the cost that HiveNetGA attempted to minimise.

Table 2. Cost functions tested in HiveNetGA.

Name	Criteria	Equation(s) for calculating criteria
Maximum Efficiency Cost Function (MECF)	1. Maximises energetic efficiency, or ratio of power consumption at the hive to power drawn from the resources	1. $\eta = \frac{P_H}{\sum P_R} = \frac{I_H V_H}{\sum I_R V_R}$
Maximum Power Cost Function (MPCF)	1. Maximises power consumption at the hive	1. $P_H = IV_H$
Maximum Power Minimum Links (MPML)	1. Minimises inverse of power (hence maximising power) 2. Minimises total link length	1. $InvP = \frac{1}{P_H}$ 2. $L_T = \sum_{i=1}^{nLinks} l_i$
Maximum Power Minimum Resource Disconnection (MPMR)	1. Minimises inverse of power 2. Minimises total link length 3. Minimises number of types of resources for which none of that type are connected to the hive (denoted as r)	1. $InvP = \frac{1}{P_H}$ 2. $L_T = \sum_{i=1}^{nLinks} l_i$ 3. $R = \sum r$

3.2.4 Breeder and Overall Algorithm Parameterisation

The parameterisation of the breeder function involved designing the overall flow of operators, and defining the probability of each, while overall algorithm parameterisation involved determining the number of networks evaluated in each generation, and the termination criteria. The choice of values for each of these was informed by existing literature on the topic, as well as testing and performance evaluation. Despite requiring a significant quantity of parameters, especially for the breeder, GAs are quite robust in their sensitivity to the values of these parameters as discussed previously, and this one was no exception. Instead, its performance was much more a result of the criteria in the cost function, which directed the search and evolutionary preference of the algorithm.

The two parameters required for the overall GA operation, which have been shown to have a more significant impact on performance (Xu et. al., 2009; Pinel et. al., 2012), are the population size, or the number of possible networks generated and evaluated each generation, and the termination criteria, which here was a set number of generations. For HiveNetGA, the population size was set to 1000 networks for the single criterion optimisation, and 1500 for the multi-criteria optimisations. These were higher than the suggested populations for similar problems in the literature (Dandy et. al., 1996), due to the possible modality of the solution space for the optimisation, and the additional criteria in the multi-criteria cost functions. Increasing the population size from 1200 to 1500 nearly doubled the computational memory use, so increasing past this was determined to be infeasible. The population was evolved over 8000 generations for all optimisations, which balanced reasonable runtime, with thorough exploration of the Pareto front for the multi-criteria optimisations, as visualised by plotting the three criteria in the cost function against one another (Fig. 9); and convergence of network structure for both multi-criteria and single criterion cost functions, as measured by the decrease in change of link length for single criterion, and for multi-criteria, the convergence of minimum and maximum link length around the average link length for all networks on the Pareto front for a given generation (Fig. 10).

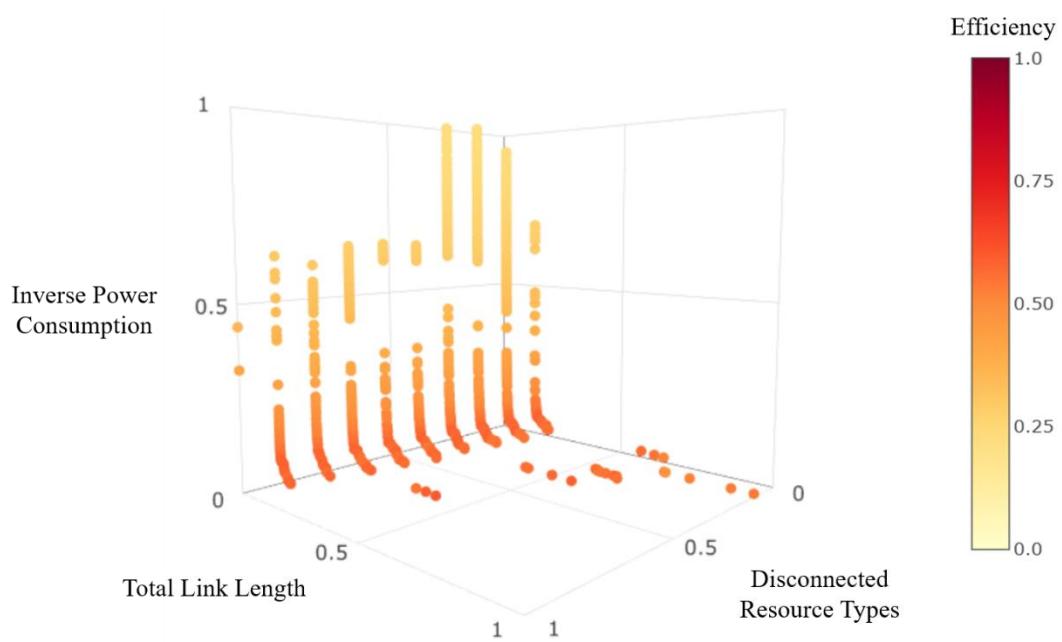


Figure 9. Pareto front for final multi-criteria breeder parameterisation. The three costs are plotted against one another on normalised axes. Compared to the other breeder parameterisations tested, this set showed the most coverage of the three criteria and contained the most networks. The seemingly more limited coverage of the Total Link Length cost is due to the outliers skewing the normalisation slightly.

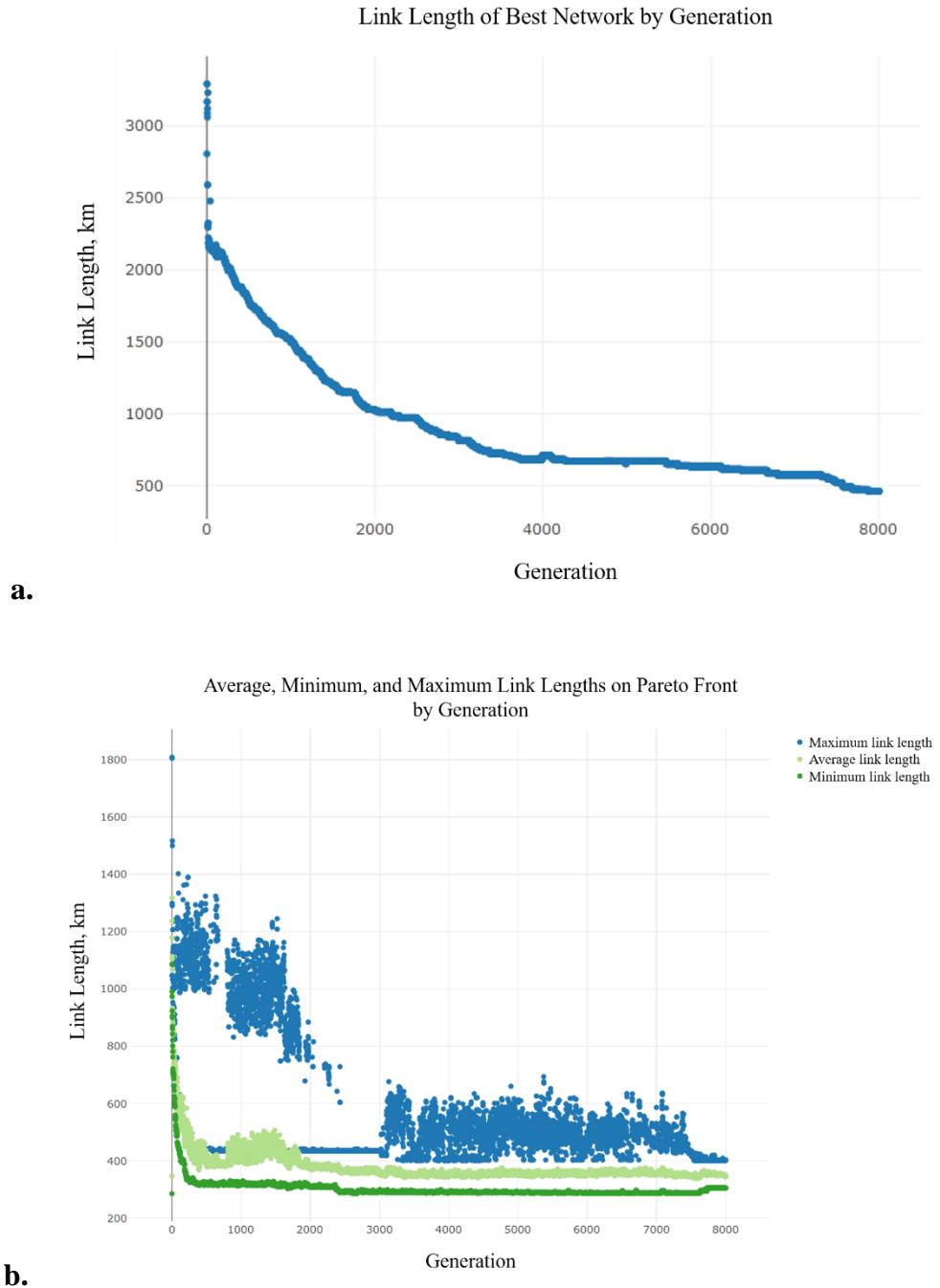


Figure 10. Link length plotted over generations for final breeder parameterisation of single criterion (a) and multi-criteria (b) cost functions. The link length shown for each generation of the single criterion optimisation is the link length of the one best network in that generation. The three link lengths shown for each generation of the multi-criteria optimisation represent the average, maximum, and minimum link length of the best networks found in that generation alone, i.e. the Pareto front from that generation.

The overall structure of the breeder function was a combination of several key features: sorting by dominance for multi-criteria optimisation (Fonseca & Fleming, 1993; Deb et. al., 2002), elitism (Goldberg, 1989) and truncation of lowest-fitness population members before selection of the breeding population (Montesinos et. al., 1999), clearing within fitness niches (Pétrowski, 1996), stochastic universal sampling (Baker, 1987), and transitioning from global to local search through annealing of genetic operator probabilities (Srinivas et. al., 1994; Smith & Fogarty, 1997). Each of these features had substantial evidence in technical GA literature and/or application-specific literature utilising GAs for network optimisation, showing its superior performance relative to the classical GA. These design choices reflect less the science behind a given domain-specific RADE network, but are rather general decisions reflecting the best methodology for single- and multi-criteria optimisations of complex problems, such as network optimisation, using GAs.

While much of the overall breeder code structure and genetic operator dynamics for single- and multi-criteria versions of NetGA (see Section 2.2.2) was retained for HiveNetGA, the specific probabilities of crossover, perturbation, and mutation, as well as the niche radius and capacity for the breeder in the multi-criteria optimisations, were adapted to fit the optimisation at hand.

Table 3. Final parameterisation of the breeder function.

Parameter	Value
Total generations evaluated	8000
Population size	1000 (single criterion), 1500 (multi-criteria)
Crossover type	Uniform
Probability of local search via crossover and perturbation	0.2, increased to 1.0
Probability of perturbation after crossover, and for each gene	1.0, decreased to 0.01
Perturbation variance	1.0
Probability of mutation for entire network, and of each gene	0.2
Number of best networks kept before creating breeding population	12
Number of worst networks removed before creating breeding population	12
Niche radius (multi-criteria only)	0.2
Niche capacity (multi-criteria only)	20

For both single criterion and multi-criteria optimisations, the initial value for the probability of employing local search, via crossover and perturbation, was lower than that found in the literature (Goldberg, 1989), at 0.2, as it increased over the course of the optimisation. The final probability of local search was 1.0, such that almost all networks in the later generations were produced via crossover and perturbation. The probability of perturbation after crossover was set at 1.0 initially, so that all crossover-produced solutions in early generations would be altered slightly, but this decreased slowly to preserve more of the good characteristics of later crossover solutions, so that the final probability of perturbation was 0.01. The perturbation variance was set to be approximately 3.5 % of the range of values for branch point locations, so that it was a small alteration when applied. This variance remained constant throughout the course of the optimisation. For networks in the breeding population that were not used in crossover, the probability of mutation of the network as a whole, and of each gene within it, was 0.2, but as the probability of crossover increased over the course of the optimisation, the likelihood of producing a network through mutation effectively decreased (Fig. 7). The number of best networks moved automatically to the next generation and the number of worst networks removed before creating the breeding population were 12 each, close to 1 % of the population for each multi-criteria and single criterion optimisations.

For multi-criteria optimisations, which included the niche-clearing mechanism described in Section 2.2.2, additional parameters for the niche radius and capacity were required. The niching radius was set as 0.2, which was about 12.5% distance between each normalised criterion for MPMR, and 15 % distance between each normalised criterion for MPML on average. The capacity of each niche was 20, or just over 1 % of the population, encouraging diversity in the breeding population. Initial estimates for these values were determined by scaling up the values of similar tests in the literature (Sareni & Krahenbuhl, 1998; Montesinos et. al., 1999) to reflect the larger population size and solution space modality. The niche radius and capacity, as with the probabilities of the other operators and the perturbation variance, were each tested individually over different values, with other parameters held constant, to determine final values.

The breeder parameterisation testing for the single and multi-criteria optimisations is summarised in Appendix B. The single criterion parameterisations were tested using

MPCF, while the multi-criteria parameterisations were tested with an early version of MPMR, each over the grassland resource distribution map. Calculation of the disconnected resources cost in MPMR was changed slightly after parameterisation of the breeder, but this would not affect which was the best breeder parameterisation. Although the multi-criteria optimisation showed greater sensitivity to the parameterisation, most of the parameterisations tested covered roughly the same Pareto front. As it would not have been feasible to examine every network generated, since most Pareto fronts returned contained thousands of networks, and it could not be determined a priori if there were network structures to actually fill each space along the Pareto front, it was more important to ensure that the Pareto front covered a range of values for each criterion in the cost function, than whether it covered the space completely. Furthermore, as this proof of concept was designed to evaluate the use of GAs for ecological and socio-ecological network modelling as a whole, as opposed to perfectly optimise the provided test case, the validity of the networks produced was of more concern than perfecting the performance of the algorithm, as long as the algorithm's performance was adequate to explore the solution space and return a range of potential solutions. The final parameterisations for single and multi-criteria cost functions were thus chosen to maximise performance and Pareto front coverage, respectively, within the overall aims of the optimisation.

3.3 Assumptions

“Essentially, all models are wrong, but some are useful.” (Box, 1979)

As with any model, the model of RADE networks presented here, comprised of generalised resource flow calculation and optimisation of a population of randomly generated networks, contains several assumptions that must be considered before testing and analysis. These include both model-level and parameter-level assumptions, with the scale of the assumption key to assessing its impact on the model performance. Model-level assumptions are those that are embedded in the overall design of the generalised RADE network model. For NetGA, these are linearity, optimality, and unlimited resources. In contrast, parameter-level assumptions are added when the model is parameterised to reflect a specific RADE network, such as HiveNetGA has been for nectar foraging networks.

The model-level assumptions are arguably the more important of the two, as they have a wider impact on the applicability and generalisability of the model as a whole. In this case, however, the model was designed to be a general model (Levins, 1966) and represent an ‘economical description of natural phenomena’ (Box, 1976), such that the assumptions represent simplifications that do not constrain its overall usefulness, if accounted for properly. The first is the assumption of linearity between inputs and outputs, as encoded in the resource flow calculations. In the networks presented here, this means that the agents, resources, and links in the network behave in such a way that the production, consumption, and loss are linear functions of the voltage and current inputs along each link and node. Moreover, the model rests on the ability to specify analogues for voltage, current, and resistance for the given system. For all RADE networks, however, there must be an analogue for the energetic charge or potential of the resource distributed, a measure of the flow of resource, and a quantification of the energetic cost of moving that resource through the medium of transport, such as pipes, veins, roads, or in this case, flight paths. These measures must follow principles of conservation and entropy generation, as discussed, and show how the system is downgradient as a whole, when all relevant energy flows are included. Finding analogues for the representative electrical components is therefore not only possible, but can also be highly instructive in its own right. Furthermore, modelling of even non-linear systems has been achieved successfully using similar methods to those presented here, when the system in question was broken down into linear components, analysed, and then recombined at larger scales using circuit equivalence theorems (Wang et. al., 2012). Other systems of known non-linear components show more linear behaviour at larger scales, allowing for simple models to accurately recreate their dynamics (Savenije & Hrachowitz, 2017). As with homeostasis and similar phenomena of self-regulation, discussed earlier, this emergent linearity validates the use of linear models even for complex systems, when either the macro-level dynamics of the system are linear, or the system can be broken into linear sub-systems.

In addition to its linearity, the resource flow methodology developed here does not allow for the quantity of current at the resources to be specified or fixed across networks, as the current drawn from each resource is dependent on the resistances and voltages of the links and nodes connected to it. Instead, the methodology represents heterogeneity in the system through different voltages at different types of resources, and at each

agent. In the generalised RADE networks modelled here, therefore, the power provided by a resource to the system is variant on how much the system draws from that resource, as opposed to being a property of the resource itself. In an idealised system, however, this is not entirely unrealistic, because as a system grows it will naturally draw more flow from its resources to sustain itself, and to compensate for growth-related transport penalties (Jarvis et. al., 2015), increasing the total power consumption of the system. Ecological theory dictates that given degrees of freedom in available resources, a system will progress toward states of higher utilisation of this free energy, via mechanisms of growth and development (Jørgensen, 2006). Similar trajectories of energy consumption of industrial society, most notably Jevon's paradox (Jevons, 1865), would suggest that human-engineered systems follow the same pattern. This would indicate that up to the limit of what they can produce, the power of resources is indeed based on what is drawn from them, resulting from a combination of their inherent potential, their location and ease with which the resource can be extracted and transported, and the flow drawn from them, modelled here as voltage, resistance, and current, respectively.

The demand-driven resource flow effectively also means that resources are unlimited, and agents always receive the amount of current that they demand. This is again due to the necessity of having the same number of equations as unknowns for the modified resource flow methodology. Although future work examining the dynamics and energetics of generalised RADE networks under constrained resources would be instructive, for the purposes herein the model operates under the assumption of representing fixed moments in time, such that the resource flow calculated is that which is occurring in the moment represented by the network, as opposed to sustained over time. Including a criterion in the cost function that encourages connection to multiple resource nodes, such as done in MPMR, helps guide the optimisation toward selecting structures that use current more equitably between resource points, and therefore rely less on the unlimited nature of the resources.

The other main model component, the GA, also introduces a model-level assumption in the form of optimality. As discussed, there is a considerable number of theoretical and empirical arguments as to the progressive optimisation of RADE networks (e.g. West et. al., 1997; Banavar et. al., 2010; Jarvis et. al., 2015), due to the selective pressure placed upon them, hence the decision to include optimisation of the networks in the

model to represent this phenomenon. Modelling the end state of a system in this way can provide insight into its potential trajectory, however, and any differences between characteristics, both qualitative and quantitative, of known networks, and the modelled, optimised versions, could be used to hypothesise about the degrees of freedom that a system has to achieve optimality, or the lags between feedback from the environment and systemic adaptation. Furthermore, as will be shown, the appearance of patterns in the explicitly optimised networks here that correspond to known networks in natural systems provides further evidence that the latter are indeed optimised to a certain level at a given moment in time, within the constraints and pressures applied to them, despite their incremental evolution.

Finally, there are also parameter-level assumptions introduced into the model by parameterising the nectar foraging network-specific HiveNetGA. These include the number, voltage, and distribution of the resources, the number and inclusion of branch points, the criteria in the cost functions, and the rules defining what types of nodes can be connected to one another. As discussed, the HiveNetGA proof-of-concept was developed as a loose parameterisation, however, using bees as a generic focal species (Watts et. al., 2010) to test the model performance overall, as opposed to the realism of the input parameters. The resulting networks, therefore, should not be taken as exact replicas of nectar foraging networks of *A. mellifera*, just as the parameters are not exact replicas of the foraging conditions experienced by a given colony. Instead, the produced networks will be evaluated as to their potential realism for nectar foraging network structures, and optimality with respect to the specified cost function criteria.

3.4 Results

To evaluate the performance of HiveNetGA, the four cost functions were run over each of the five resource distribution maps. The two single criterion cost functions were each run with the two versions of the mutation operator, and the two multi-criteria cost functions were each run with 0.5 and 0.75 initial probability of connection. The resulting best networks were evaluated to assess their similarity to known foraging dynamics of *A. mellifera*, and the overall range of network structures produced. To validate the results, the single criterion cost functions were run again with the second version of the mutation operator, and the multi-criteria cost functions were run again

with each initial probability of connection. These validation runs were then compared to the original test runs, through visualisation and/or quantitative analysis as appropriate to the cost function. The visualisations were generated using the R packages rgl version 0.99.9 (Adler & Murdoch, 2018) and RColorBrewer version 1.1-2 (Neuwirth, 2014), and the graphs of the quantitative analyses were produced with the R package plot.ly version 4.7.1 (Sievert et. al., 2017).

3.4.1 Single Criterion Cost Functions

The networks produced by the first two cost functions, MECF and MPCF, which maximised efficiency and power, respectively, are shown below (Fig. 11). By drawing the branch points to directly underneath the hive and nearby resources, and disconnecting many of the links to further resources, the link length and therefore resistance-driven losses have been reduced considerably. The networks adhered to a mostly radial burst pattern centred on the hive, and the two cost functions produced very similar networks for the five resource distribution maps. The results are shown in detail in Table 4. Overall, the average efficiency across all resource distribution maps for MECF was 0.776 (± 0.029 SE) for the five resource distribution maps tested, compared to an average efficiency of 0.750 (± 0.023 SE) for MPCF, and the average link length for MECF was 786.795 km (± 146.670 km SE) compared to 865.734 km (± 137.589 km SE) for MPCF. Power was not measured for MECF, but the average was 122.34 (± 5.11 SE) for MPCF.

Table 4. Results for first round of testing MECF and MPCF cost functions.

Cost Function	Resource Distribution Map	Power (J sec ⁻¹)	Efficiency	Link Length (km)
MECF	Grassland	NA	0.835	532.781
MECF	Grassland farmland	NA	0.791	760.823
MECF	Grassland park	NA	0.839	570.609
MECF	Grassland woodland	NA	0.753	645.795
MECF	Woodland	NA	0.661	1423.966
MPCF	Grassland	139.925	0.691	463.422
MPCF	Grassland farmland	119.260	0.753	1175.869
MPCF	Grassland park	130.317	0.781	1057.849
MPCF	Grassland woodland	114.157	0.830	1110.149
MPCF	Woodland	108.042	0.700	521.379

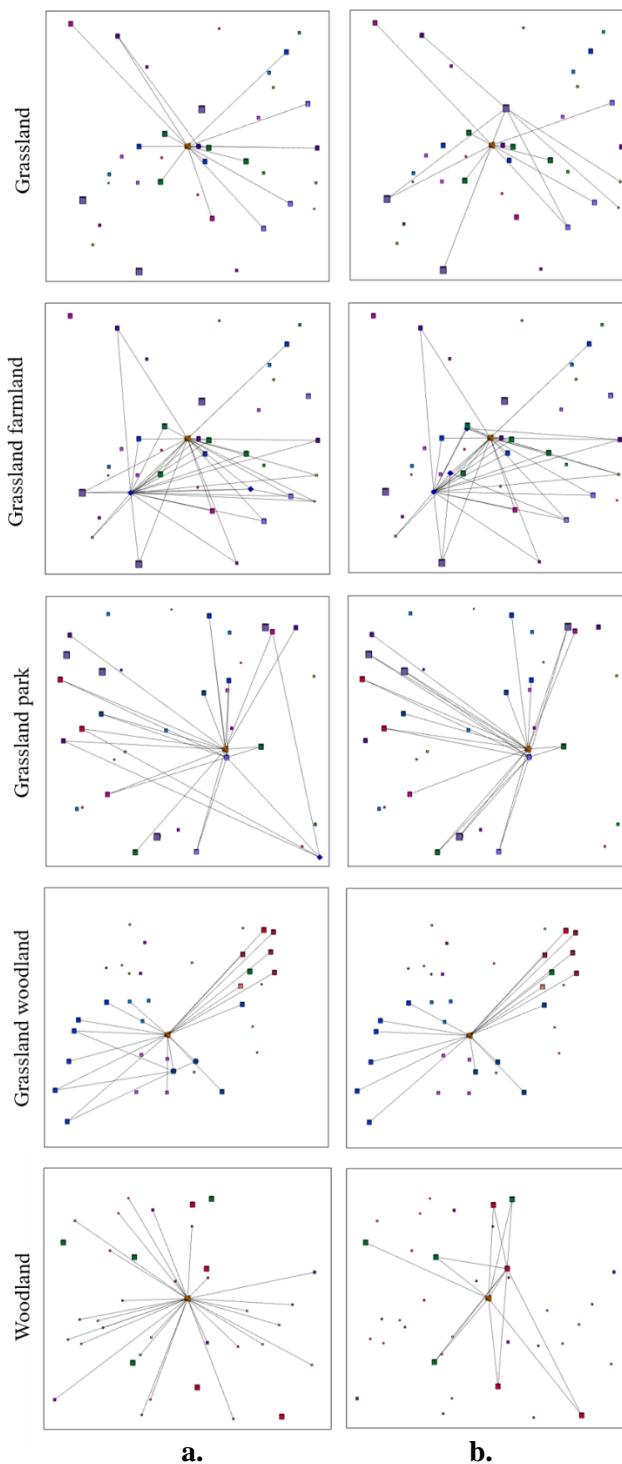


Figure 11. Networks produced by first round of testing MECF (a) and MPCF (b) cost functions. The hive is the orange tetrahedron located close to the centre of each network, branch points are black spheres, and resources are coloured squares. The colour of the resource denotes its type, as appropriate for the listed habitat, and the size denotes its comparative nectar sugar concentration.

As the mutation operator in the breeder was causing HiveNetGA to disconnect links with a high frequency throughout the optimisation, in order to reduce resistance, it was changed as described previously in Section 3.2.2. This encouraged exploration of reducing resistance by optimising existing links, as opposed to removing them. The results of maximising power and efficiency with the changed mutation operator are shown in Fig. 12. While maximising power tended to produce networks close to a radial burst pattern, maximising efficiency resulted in the network spreading its branch points over the maximum distance across the topology, potential reasons for which were explained previously in Section 3.2.3.2. The runs were performed twice for each cost function, with the second round acting as a validation of results of the first round. The similarity of visualised networks (Fig. 12) and qualitative results (Table 5) between the test and validation runs suggest the robustness of the outcomes. Overall, for the test runs, MECF produced networks operating at an average of 0.469 (\pm 0.034 SE) efficiency with an average total link length of 2516.804 km (\pm 81.594 km SE), while MPCF produced networks with an average of 0.332 (\pm 0.046 SE) efficiency, 98.637 J sec⁻¹ (\pm 0.046 J sec⁻¹ SE) power, and 1844.025 km (\pm 71.863 km SE) link length.

Table 5. Results for second round of MECF and MPCF cost functions.

Resource Distribution Map	Cost Function	Power (J sec ⁻¹)		Efficiency		Link Length (km)	
		Test	Validation	Test	Validation	Test	Validation
Grassland	MECF	NA	NA	0.570	0.525	2450.945	2852.213
Grassland farmland	MECF	NA	NA	0.462	0.507	2806.758	2817.569
Grassland park	MECF	NA	NA	0.473	0.501	2375.789	3051.193
Grassland woodland	MECF	NA	NA	0.502	0.492	2309.895	2452.764
Woodland	MECF	NA	NA	0.336	0.339	2640.634	2435.587
Grassland	MPCF	116.537	117.535	0.204	0.306	1757.534	1644.966
Grassland farmland	MPCF	96.047	98.606	0.371	0.360	2069.903	2016.174
Grassland park	MPCF	117.033	117.848	0.461	0.440	2004.314	2089.429
Grassland woodland	MPCF	91.867	91.593	0.407	0.422	1696.430	1675.326
Woodland	MPCF	71.702	71.250	0.219	0.187	1691.945	1842.313

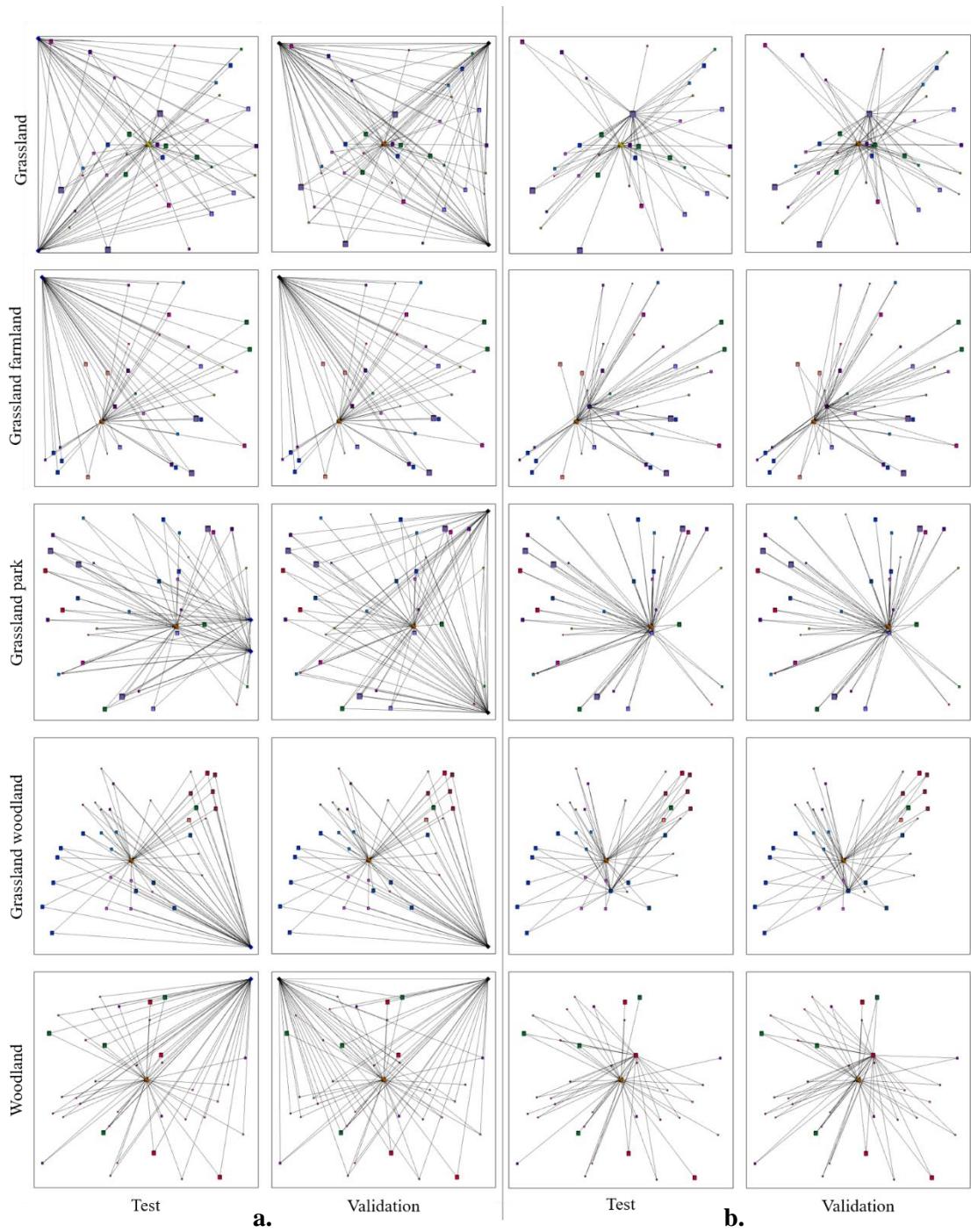
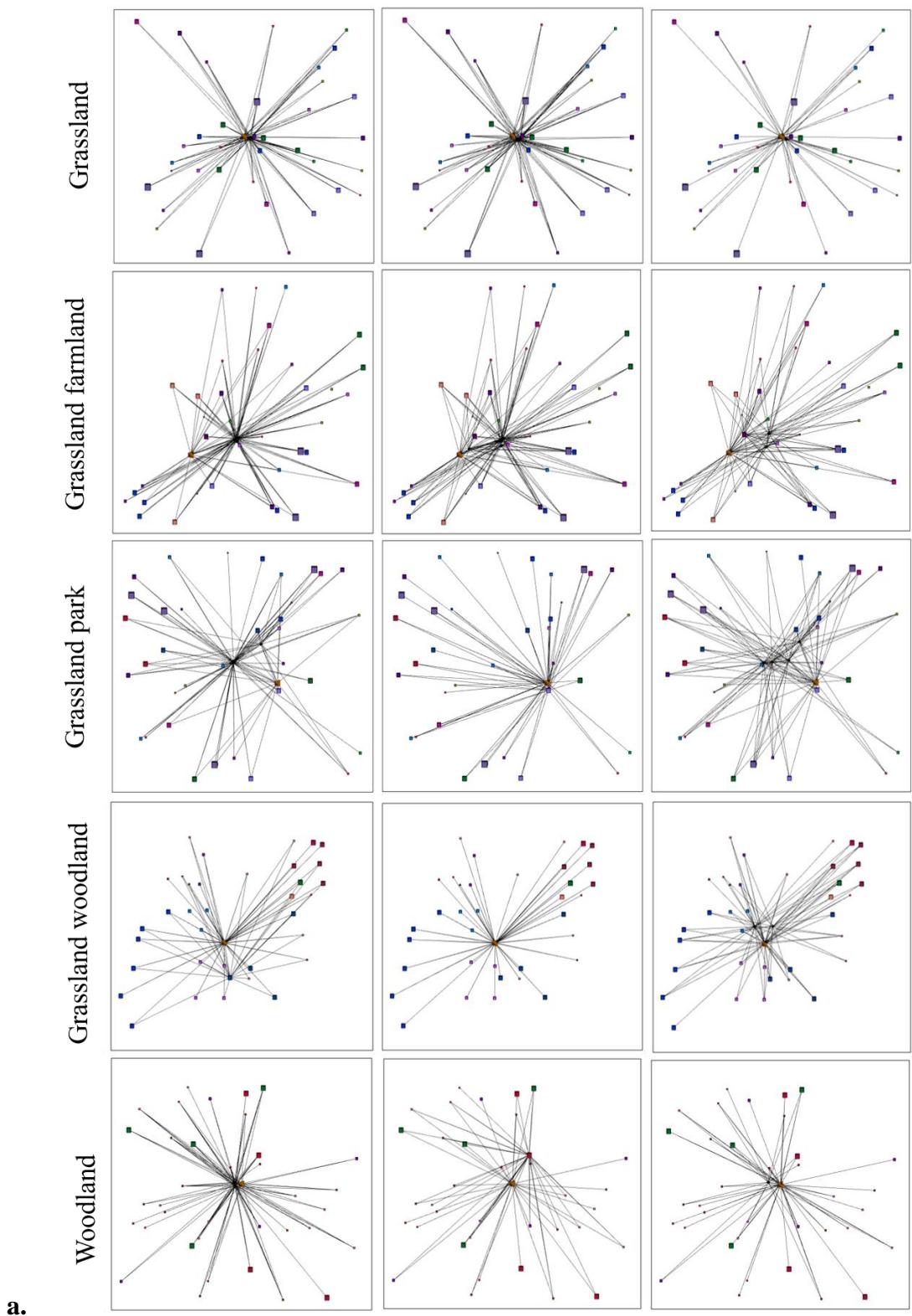


Figure 12. Networks produced by second round of testing MECF (a) and MPCF (b) cost functions. Each cost function was tested over the five resource maps (grassland, grassland farmland, grassland park, grassland woodland, and woodland), each of which contains resource points that reflect the species that a bee is likely to encounter in that habitat.

3.4.2 Multi-Criteria Cost Functions

The first multi-criteria cost function, MPML, attempted to maximise power consumption by minimising its inverse, and minimise total link length. This was tested over each resource distribution map, with initial probabilities of 0.5 and 0.75 for a link to occur between any two nodes, and the same mutation operator as the second round of the single criterion cost functions, which did not remove links. A qualitative analysis was performed by plotting the Pareto fronts of each test, identifying a selection of networks at approximately evenly distributed points along the Pareto front, and visualising the placement of the resource, hive, and branch point nodes, and the links between them. A sampling of these network visualisations for each of the five resource distribution maps is shown in Fig. 13. For 0.75 initial probability of connection, the majority of the networks visualised (210 of 259, 81.081 %) across all five resource distribution maps closely resembled a radial burst pattern, with most if not all of the resources connected, and the branch points clustered on or near the centre of the resource distribution map (Fig. 13a). For the grassland and woodland maps, the hive was located centrally in the space, so many of the branch points were directly beneath it. In the other non-centred maps, the branch points clustering near the centre acted to create a radial burst pattern. Although there were some more branched networks in the optimisations where there was only a 0.5 initial probability of connection, 120 of the 161 (74.534 %) visualised networks across all distribution maps still displayed something close to a radial burst pattern (Fig. 13b).



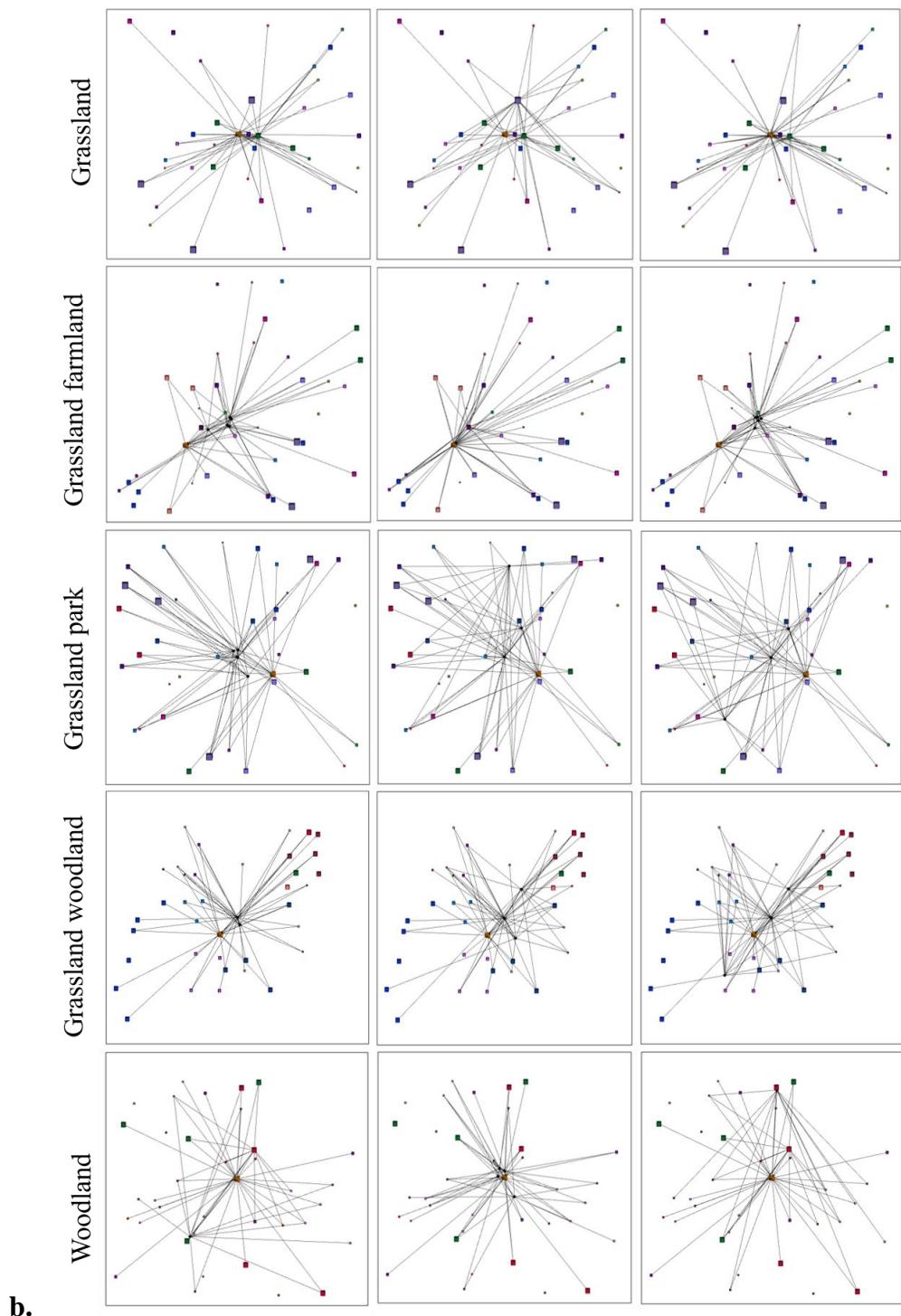
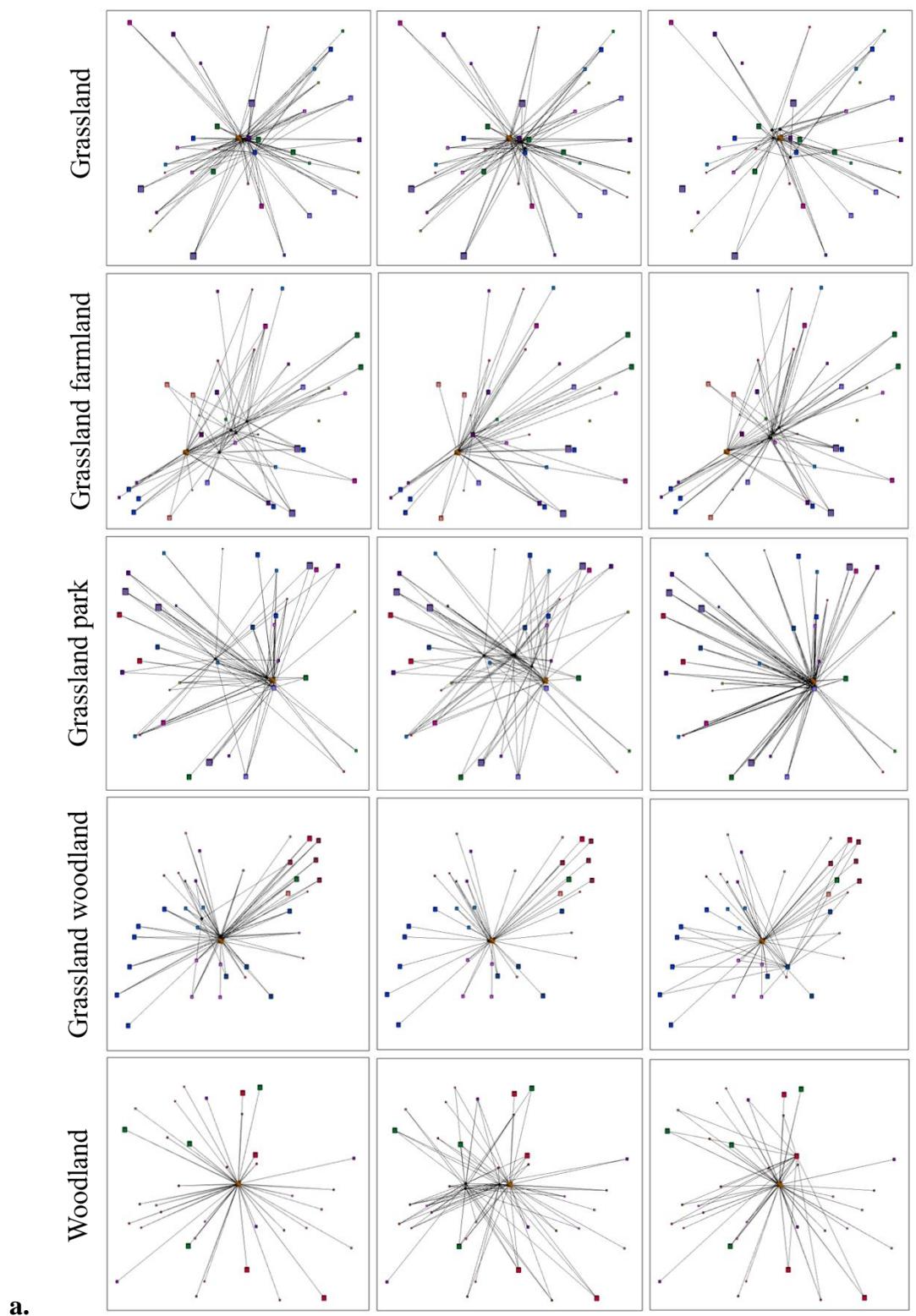


Figure 13. Network visualisations for MPML cost function. Shown with initial probability of connection of 0.75 (a) and 0.5 (b). Each connection probability was tested over the five resource maps (grassland, grassland farmland, grassland park, grassland woodland, and woodland), which contained resource points parameterised to reflect the species that a bee is likely to encounter in that habitat.

The final cost function, MPMR, which maximised power consumption by minimising its inverse, and minimised both link cost and the number of resource types to which the hive was not connected, was also tested over each resource distribution map for initial link connection probabilities of 0.5 and 0.75. As with MPML above, the networks with a 0.75 connection probability produced more radial burst patterns centred on the hive, or on a clump of branch points in the centre of the resource distribution map, if the hive was off-centred (Fig. 14a). The networks were highly connected, with only one or two resource points disconnected. These were usually resources of types where there were multiple points of the same type from which the hive could choose to connect, in order to avoid incurring a large resource disconnection cost. In the networks with 0.5 initial probability of connection, branching patterns were much more common, as the network utilised branch points to connect more distant resources to the hive with less links (Fig. 14b). While the resource distribution maps with the hive centred tended toward more radial burst networks still, but with less connection overall, the optimisations with off-centred distribution maps produced networks with a diversity of branching structures.



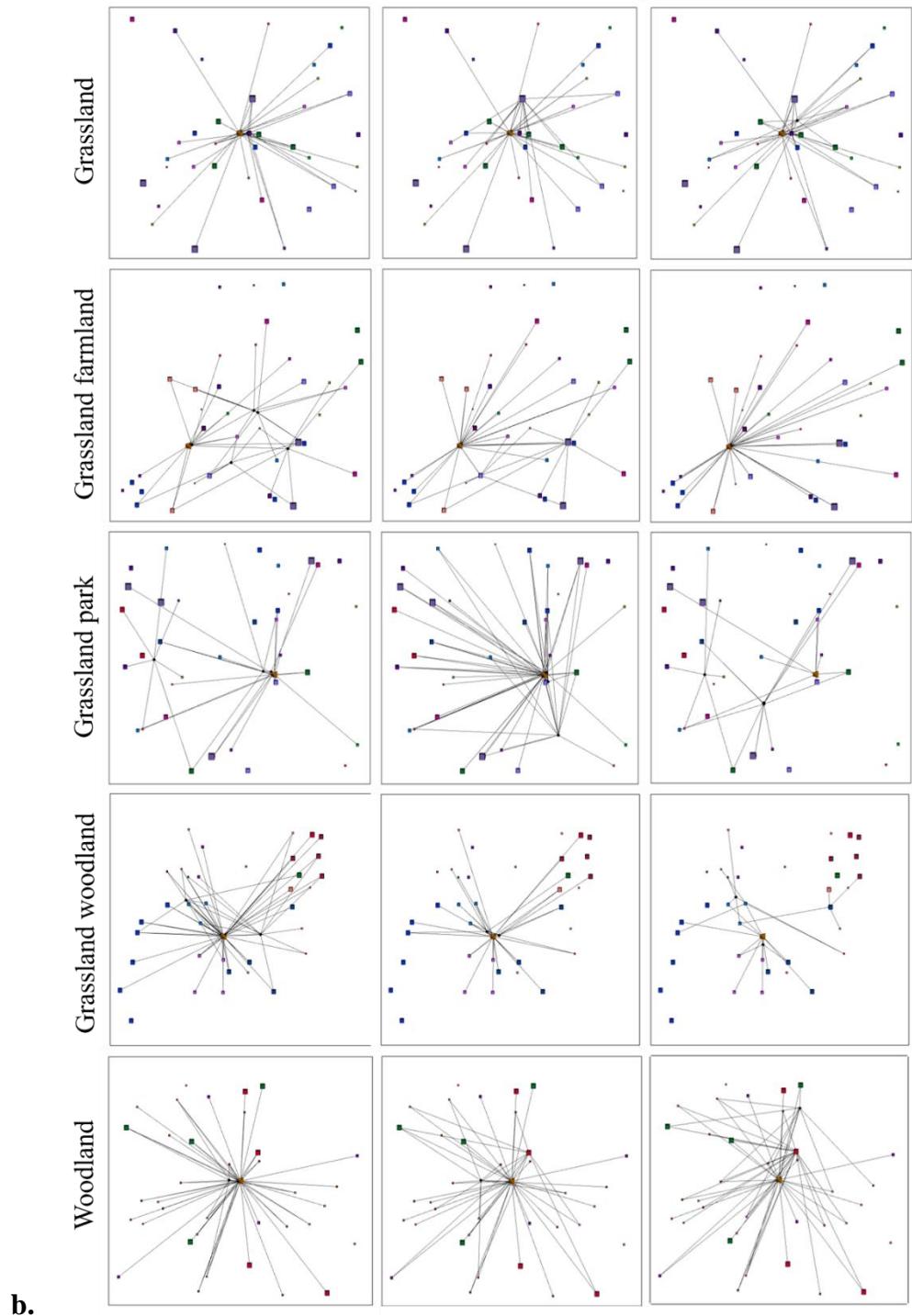


Figure 14. Network visualisations for MPMR cost function. Shown with initial probability of connection of 0.75 (a) and 0.5 (b). Each connection probability was tested over the five resource maps (grassland, grassland farmland, grassland park, grassland woodland, and woodland), which contained resource points parameterised to reflect the species that a bee is likely to encounter in that habitat.

To quantify the degree to which a multi-criteria network was branching, defined as the branch points being distributed apart from one another and the hive in space, the mean of the Euclidean distances was calculated between each branch point and each other branch point, and each branch point and the hive, for each network on the Pareto front. This also allowed for a form of structural analysis for each network on the Pareto front, as it was not feasible to visualise every network. Plots of this branching spread measure for each resource distribution map and level of connectivity for the two multi-criteria cost functions are shown in Fig. 15. The distribution of the measures of spread is slightly closer and more overlapping in the higher connectivity networks, indicating a higher frequency of similar structures across the Pareto fronts for the two cost functions. In the networks with only 0.5 initial probability of connection between any two nodes, however, MPMR shows higher branching spread measures for the resource distribution maps where the hive was off-centred, with medians 5.267 (IQR 5.015 – 6.018, grassland farmland), 5.241 (IQR 4.934 – 6.431, grassland park), 5.762 (IQR 4.418 – 5.962, grassland woodland) as compared to those for MPML: 1.667 (IQR 1.483 – 2.197, grassland farmland), 3.156 (IQR 1.971 – 3.478, grassland park), 0.168 (IQR 0.009 – 2.110, grassland woodland).

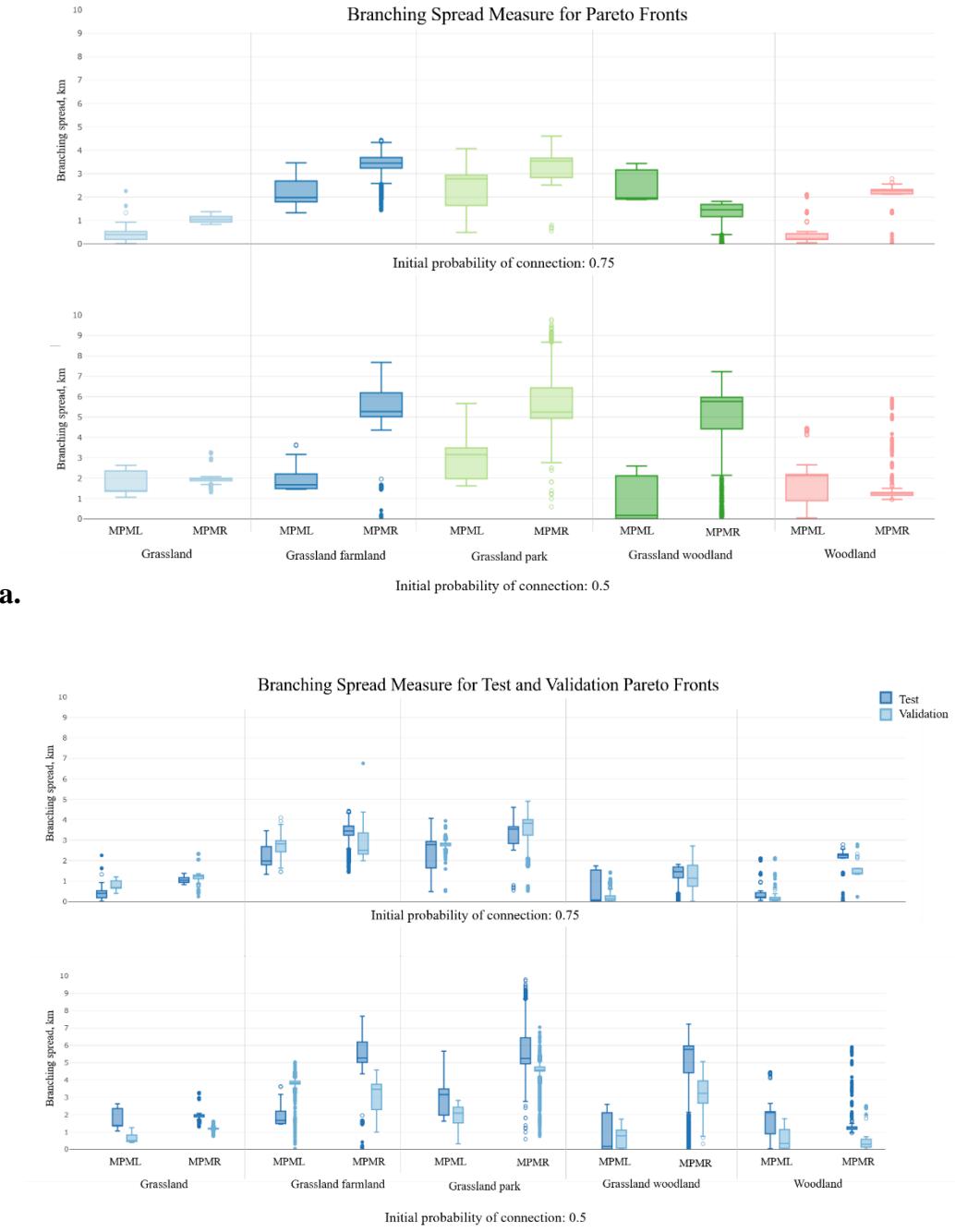


Figure 15. Branching spread measures for Pareto fronts. The branching spread measure, defined as the mean Euclidean distance between each branch point, or non-demand node, and the hive, and each pair of branch points, was used to represent the overall ‘spread’ of the network, since visualising each of potentially thousands of networks along the Pareto fronts was not feasible. Shown here is the distribution of branching spread measures along the Pareto front for each multi-criteria cost function tested (a) and as compared to the validation runs (b).

To validate the performance of HiveNetGA on MPML and MPMR, all simulations combining each combination of cost function, connectivity, and resource distribution map were repeated. To compare the test and validation runs, the same branching spread measure was plotted for all validation runs as well (Fig. 15b). This acted as a proxy for comparing the structures of the networks returned by each run, without visualising each network along the Pareto fronts. The optimisations with an initial probability of connection of 0.75, have fewer degrees of freedom to explore due to a slower rate of disconnection through crossover. As such, more of these are fully connected radial burst networks, making it easier for HiveNetGA to locate the same optimal networks in each run. In contrast, the optimisations with a lower initial probability of connection of 0.5 can explore more disconnected, branching structures, which are harder to replicate precisely, hence the larger difference between the test and validation runs. The similarity of overall range of branching spread that each Pareto front returns, however, indicates that HiveNetGA identifies a similar range of structures, even if not at the same frequency. Overall, the similarity of the range of network structures between the test and validation runs, despite the many combinations of possible branch point locations and link configurations, demonstrates the robustness and consistency of the optimisation.

Additionally, there were positive and mostly high correlations for all of the multi-criteria optimisation runs between link length and power consumption across the Pareto front, as shown in Table 6, indicating that radial burst networks with longer total link lengths produced higher overall power transfer than networks with more branching structures. The less connected networks, as produced by the lower initial probability of connection, showed a very similar or weaker relationship between power and link length in all but one instance (MPML woodland). As shown in Fig. 17, this cost function/resource distribution map pairing shows a visually very similar relationship between total link length and power consumption, but the Pareto front for an initial connection probability of 0.5 contained 704 networks, as opposed to the Pareto front for an initial connection probability of 0.75, which contained only 242 networks due to the fewer degrees of freedom for more connected networks. This difference in Pareto front size likely affected the correlation.

Table 6. Correlation between power and link length for multi-criteria cost functions.

Initial Probability of Connection	Cost Function	Resource Distribution Map	Power/Link Length Correlation
0.75	MPML	Grassland	0.614
		Grassland farmland	0.974
		Grassland park	0.923
		Grassland woodland	0.859
		Woodland	0.790
	MPMR	Grassland	0.936
		Grassland farmland	0.866
		Grassland park	0.914
		Grassland woodland	0.604
		Woodland	0.845
0.5	MPML	Grassland	0.667
		Grassland farmland	0.939
		Grassland park	0.758
		Grassland woodland	0.731
		Woodland	0.949
	MPMR	Grassland	0.688
		Grassland farmland	0.813
		Grassland park	0.283
		Grassland woodland	0.688
		Woodland	0.749

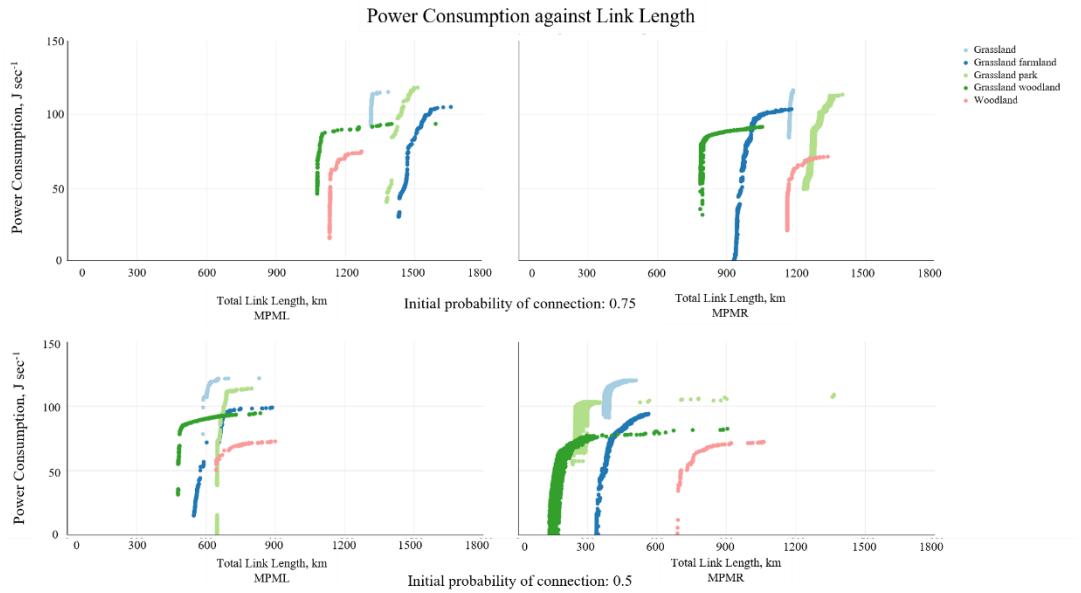


Figure 16. Power consumption (J sec^{-1}) against total link length (km) for MPML and MPMR. The power consumption (W, or J sec^{-1}) against link length for all members of the Pareto front, for both multi-criteria cost functions. As it would not have been feasible to visualise all networks along the Pareto front individually, this allowed for an overview of the positive correlation between length and power consumption, for all resource distribution maps.

4. Discussion

4.1 Interpretation of Results

The network structures and frequencies of each that were produced by the four cost functions demonstrate both the ability of HiveNetGA to model and optimise networks to meet a variety of criteria defining optimality, and the similarity of the structures that are optimal for the different criteria. Including the perhaps initially surprising results generated in the second round of testing MECF (Fig. 12a), which Section 3.2.3.2 and below demonstrate is both explicable and even predictable in retrospect, the overall optimisation performed as expected, mostly shortening and/or removing links to maximise consumption while minimising resistive losses. In order to further evaluate the results, they are compared here to known characteristics of foraging networks. Foraging routes themselves are not usually mapped explicitly, due to the inherent difficulty in following individual bees over potentially long distances. A great deal is known about the resource utilisation and energetics of foraging and pollination by *A. mellifera*, however (Seeley, 1995), making it possible to qualitatively assess whether a given network could be a realistic representation of spatially-mapped foraging efforts for a colony.

The first round of testing the two single criterion cost functions, MECF and MPCF, and the multi-criteria cost functions when run with the lower initial probability of connection, each showed high levels of disconnection in the optimised networks. This is not necessarily unrealistic for foraging networks, however. At any given point, a forager bee is only gathering nectar from one patch, and relies on the waggle dances of other foragers and scouts to navigate to another patch (Seeley, 1995), should hers become energetically unprofitable in supply or quality (Rivera et. al., 2015). As such, the colony may only exploit a limited supply of the available floral resources available to them at a certain time, favouring those that are most energetically profitable (Visscher & Seeley, 1982). Therefore, only connecting to the most energetically profitable resources, as measured by quality of the resource and energetic cost of acquisition, is likely a realistic attribute of a foraging network. In terms of the model itself, both the higher rate of disconnection, and initially lower probability of connection, produced similar results, but the lower initial probability of connection likely converged more

quickly on optimal structures, as the algorithm was not continually reducing the number of links with which to create those structures.

The second round of the single criterion cost functions (Fig. 12) produced both typical radial burst patterns and the radial burst with extended branch points. As discussed in Section 3.2.3.2, this is due to the optimisation attempting to reduce the effect of current-driven voltage drop when it could not otherwise change the inherent resistance of the links, such as through increasing strength. Adding links in this way to decrease the concentration of current per link is similar to building a bypass to alleviate traffic bottlenecks on a busy road. The resistance-based losses experienced by foraging honey bees, however, are more a function of distance travelled than quantity of nectar carried, as *A. mellifera* have developed behavioural adaptations to avoid energetic losses caused by carrying heavy weights, such as only filling their crop, or ‘honey stomach,’ partially (Kacelnik et. al., 1986). This is a tactic that is more common for shorter flights, while longer flights tend to elicit fuller crops. In the networks produced here, this would be represented by the longer links having more current flowing down them, despite higher length-based resistance, such that all links would carry relatively similar currents for a single bee. As most foraging flights are within 1-2 km of the hive, and almost all within 6 km of the hive (Seeley, 1995), however, at the colony-wide level, there would still be higher flow from the shorter links, as modelled here. Due to these weight-restricting adaptations, the networks with extended branch points are likely not realistic representations of nectar foraging networks. The addition and extension of links is an explicable and realistic phenomenon, though, based on the equations governing physical flows that were used in modelling, and the constraints on degrees of freedom the network had to reduce resistance.

In contrast, the radial burst networks (Fig. 12 - 14) produced by the optimisation, as could be expected given the centrally- or nearly centrally-located hive, is more likely optimal for *A. mellifera*, as each forager only gathers nectar from a single species of floral resource per trip as noted previously, and would likely attempt to fly as directly as possible between the nectar sources and hive. Radial burst networks, with a unique link between each resource and the hive, would appear costlier than path-reusing branching networks. For foraging networks with minimal to no ‘construction cost,’ however, it would be more energetically efficient to fly directly between the hive and

the target resource. The navigation costs of finding a new resource, which are in this case the closest analogue to construction costs, are mostly felt by the forager or scout discovering the patch. She then provides directions to foragers who come after her (Seeley, 1995), hence limiting the energetic impact of this initial stage. Furthermore, the links between the resources and hive do not have to be maintained except in memory, which further limits the need for path re-use. Links making ‘bee lines’ to connect the hive to individual resources directly, are therefore a realistic outcome, and the frequency with which HiveNetGA produced something resembling this pattern denotes the robustness of its optimality within the provided cost constraints.

The branching structures displayed in some of the less connected networks optimised by the MPMR cost function (Fig. 14b) are reminiscent of scale-free networks (Barabási, 2016), wherein the hive and branch points act as ‘hubs’ with a high node degree, or number of connections, with ‘spokes’ or links to the resources. Over larger distances, these also appear as the hierarchical or fractal branching patterns seen in systems as diverse as mammalian vascular systems, tree roots and branches, and river networks (West et. al., 1997; Rodriguez-Iturbe & Rinaldo, 2001). These networks are an efficient means of connecting up distant nodes with a shorter total link length. In this optimisation, the lack of link strength meant that these networks suffered higher energetic losses, due to the current flow being concentrated onto fewer links. In real-world networks, however, these links combining current from multiple resources would be preferentially strengthened if possible to decrease the resistance along them. To revisit the road metaphor used before, this would be akin to widening heavily utilised roads to reduce traffic bottleneck. As bees do navigate with landmarks, they potentially follow branching structures such as these to navigate to more distant resources. Studies on the spatial memory of bees has shown that they are able to recognise the same landmark from multiple directions (Menzel et. al., 2005), allowing a shared landmark to point them toward multiple sources. Navigation to nectar sources is mostly done via following waggle dances (Seeley, 1995), however, making a branching pattern more common for route-finding on the way home from an unfamiliar resource, or linking very closely co-located points of the same species. Furthermore, many of the networks involving branching placed the branch points directly atop different resource points, effectively cheating the rule preventing different types of resources from connecting to one another. As such, these networks are likely less realistic for nectar foraging

networks, but their inclusion along the Pareto front points to both the effectiveness of HiveNetGA at identifying and returning network structures known to be optimal given the criteria, and further demonstrates the robustness of these structures' optimality under different criteria and connectivity levels. Overall, however, the majority of the networks produced by HiveNetGA reflect several likely characteristics of honey bee foraging patterns, despite the approximation of its parameterisation.

4.2 Overall Algorithm Performance

Although approximately parameterised to replicate nectar foraging conditions for *A. mellifera*, the proof-of-concept also provides several insights into the use of GAs for RADE network modelling and optimisation in general. These observations also point to some interesting hypotheses about the dynamics of RADE networks and potentially fruitful areas for future study.

Possibly the most important general conclusion that can be drawn from the case study presented here is that GAs are extremely powerful optimisers. This was demonstrated here by the results of the second round of testing MECF (Fig. 12a), where HiveNetGA clearly showed that the optimal result for maximising efficiency of a highly connected network was not what might have been expected. Although this was easily enough explained in retrospect, HiveNetGA was able to identify this relationship between current and voltage drop, as well as the more obvious relationship between resistance and voltage drop, and optimised the network to balance minimising both contributions to power loss. This was despite the algorithm only truly basing selection and breeding decisions on the ratio of power used to power generated, and matching network characteristics to different levels of that ratio. GAs seem to be able to deduce more complex rulesets from simple cost functions, and return both approximations of real systems, and suggestions of how 'possible, but non-actual, phenomena with a certain causal structure will behave' (Weisberg, 2006) such as branching structures (Fig. 14b). This makes them extremely flexible, and potentially able to replicate emergent properties of RADE networks resulting from interactions of different cost criteria and degrees of freedom, which would be onerous or impossible to work out a priori.

In the optimisations presented here, these branching networks were Pareto optimal in that they had the lowest link costs and disconnection costs, but also lower power

consumption. This demonstrates that the ability to decrease resistance by increasing the strength of a link or otherwise changing its inherent resistance, offsetting the losses due to increased current, is necessary for these branching structures be so prevalent in systems theorised to be guided by natural selection for higher energy consumption, unless the energetic cost of link addition and maintenance is considerably higher than that of resistive loss due to increased current flow. Further work in this area would be instructive to evaluate these interactions between cost and constraint via degrees of freedom, and the ability of NetGA to optimise within different levels of each.

The power of algorithmic optimisation via evolutionary algorithms such as GAs is almost exclusively dependent on this cost function. This somewhat reduces the importance of extensive breeder parameter testing and sensitivity analysis, although those are still relevant. More notably, however, it makes it potentially problematic to optimise solutions when the costs constraining the production of those solutions are difficult to identify or calculate. If an extremely high level of accuracy of results is required, it is important that the constraining costs are able to be identified and calculated to that same level of precision. As stated above, though, the ability of the algorithm to find the optimal solution for a given cost function can provide interesting insights into what is optimal, and avenues for further study. Furthermore, for generalised RADE networks, approximations within reason are often accurate enough to analyse spatial dynamics and overall patterns, and provide estimates of the energetic costs of the networks in question. An inductive approach to identifying the costs constraining RADE network development could also be used: by using a weighted sum of costs to form a single criterion cost function, methodically testing a range of weighting combinations, and comparing the dynamics of the resulting networks with real-world RADE networks, it may be possible to identify generalised principles governing the weights or priorities that different RADE networks assign to different costs, such as construction, maintenance, power consumption, and energetic efficiency, and the thresholds of weights required for systemic structural change in what is considered optimal. This could also allow for further validation, by providing weightings that are known to be accurate for a given system, and comparing the resulting network with real examples of networks in that system.

The cost functions used in the nectar foraging proof of concept rest on the modified resource flow methodology, as developed for general RADE network modelling and analysis. The development of this methodology allows for easily calculating the production, consumption, and loss in a network, in a way that is consistent with the energy conservation and entropy production imperatives of the first and second laws of thermodynamics, and takes into account the effect of spatial network size and distance between components. The evidence of its effectiveness through optimal results, both those hypothesised to occur, and those arising from extended derivations of the equations used in its calculation, is one of the most important outcomes of the work here. As all physical resource flows are subject to these laws of thermodynamics, this methodology is applicable to any generalised, conserved physical resource flow, provided that force, or voltage; flux, or current; and resistance analogues can be identified. Furthermore, the demonstration of the downgradient flow of all energy, provided that the boundaries of the system in question are drawn in space and time to include all relevant energy inputs, is an important consideration when determining how to model RADE networks, and analysing the energetics of the systems that contain them.

Although excellent at modelling these systems-level dynamics at the macro-scale, such as foraging outcomes for a whole colony of bees, GAs struggle with modelling the emergence of systems-level dynamics from the interactions of individuals or agents, due to their parallel, re-combinative search strategy. This may be another reason why maximising efficiency, although empirically demonstrated at least at the level of the individual bee, shows such odd results when applied at the colony level, as done in MECF. These individual-level models are better simulated by an agent-based model, which can display systems-level characteristics as emergent properties, if the agents and their interactions are parameterised correctly (Gilbert, 2008). Agent-based models are also more able to replicate phenomena such as Hebbian learning (Schoenharl, 2005), or the selective strengthening of frequently utilised links between nodes, which may make them better equipped handle the degrees of freedom associated with the addition of link strength. This is in part due to their strategy of incrementally evolving a single solution over time, as opposed to the parallelised search of an evolutionary algorithm like the GA. As such, it is important to note whether the model of interest involves explicit optimisation is of a systems-level characteristic, or simulation of an individual

characteristic hypothesised to result in a collective optimum, when designing a model. GAs are excellent at the former, however, and can provide interesting directions for further study to determine what individual-level characteristics and selective pressures produce the systems-level optimum that is observed.

Perhaps one of the most interesting and understudied reasons for the emergence of these systems-level dynamics, that allows modelling of a diversity of even distributed or decentralised RADE networks such as honey bee nectar foraging from a systems-level perspective, is the role of information in these networks. As introduced previously, information is a crucial part of all RADE networks, whether it is the resource explicitly acquired and/or distributed, embedded in the infrastructure facilitating the acquisition and distribution, or as a coupled flow with the resource being transported. Information about the spatiotemporal location and availability, use, and quality of a resource is critical for the development and improvement of all RADE networks, and measures have been put forward for quantifying the information content of the structure of a network. More accurate accounting of the energy used and saved due to increasing the information flows and content of a network is needed to better quantify the role of information in commonly observed RADE network characteristics and dynamics, and to assess how changing information dynamics of a network could possibly influence its resilience, equity, or sustainability. Furthermore, study in this area could help shape efforts to explicitly integrate information stocks and flows in future models of RADE networks, increasing their accuracy in modelling current system state.

Finally, besides the importance of cost function parameterisation and allowed degrees of freedom, the case study also provided insight into how necessary modifications and extensions to the general NetGA model could allow it to be used for modelling specific types of RADE networks. As discussed above, the criteria in the cost function, and if applicable, the weighting of these criteria, is likely the most crucial for determining the realism of the outcome of the optimisation. While not always necessary for quantitative characteristics of the optimised networks, such as power consumption, to replicate those of real networks with a high degree of precision, the more precise and comprehensive the identification and calculation of costs, the more accurate the optimisation. Beyond this, however, for RADE network modelling and optimisation, there are several other parameters to consider: at the minimum, this could include the number and mobility of

the resource users or agents, the number and mobility of branch points, the topology of the resource distribution and underlying space filled by the network, and the analogue and quantity for voltage supply and current demand at the resources and agents, respectively. Further parameterisation would increase the accuracy and specificity of the optimisation, but could lead to overtraining, which would limit the ability of the model to represent a range of situations. Whether this generalisability is necessary would depend on the research question at hand (Levins, 1966). For the proof-of-concept here, a level of generalisability was important to assess the overall performance of the network optimiser, so it could be determined whether it would be suitable for other types of RADE networks. Its performance suggests that future work applying it to other case studies, and more general theoretical work, is indeed merited.

5. Conclusion and Future Work

This thesis explored the creation and use of a modified resource flow methodology, nested within an optimisation algorithm, to model generalised resource flow between heterogenous, spatially distributed points of supply and consumption. This was further parameterised to reflect approximate foraging conditions experienced by *A. mellifera*, and the resulting networks were evaluated as to their possible realism in representing foraging networks. The analysis suggests that this work shows considerable potential in the modelling of both generalised and specific RADE networks, for theoretical and practical applications. Several key findings from this work include:

1. The modified resource flow methodology, as adapted from electrical load flow analysis, is a spatially-explicit, flow-conserving means by which generalised resource flows can be modelled. By identifying an analogue for current, voltage, and resistance in the system, and the supply and demand of voltage and current at the resource and agent nodes, respectively, the modified system of equations can solve for the force, or voltage, and flux, or current, at each node and link. This is a new technique for modelling generalised, directed flow between complex networks of single or multiple points of resource supply and consumption, and conceptualising the necessity of downgradient energy flows in all systems, through accurately drawn systems boundaries. The explicit incorporation of thermodynamic laws through the equations used makes the methodology more realistic for calculating energetic cost of transportation through physical networks than other commonly used network metrics.
2. Genetic algorithms are excellent systems-level optimisers, and therefore are a useful technique for optimising resource networks in ecological and socio-ecological systems. The necessity of specifying a comprehensive, accurate cost function raises some difficulty for systems for which the costs are harder to identify and/or calculate. The algorithm does show an ability to seemingly deduce more complicated rules from simple cost functions, however, which allows it to model difficult to predict behaviour, potentially arising from interactions of constraints and/or degrees of freedom.

3. The inclusion of known resource network structures, such as branching and radial burst, in an explicitly optimised system, simultaneously demonstrates the optimality of these structures, and the good performance of the optimisation algorithm. The frequency of these structures within the Pareto front indicates a robustness to their optimality across different cost functions, which is further evidenced by their prevalence in a diverse array of natural and human-engineered networks.
4. The lower power consumption by the branched networks, and the stretching out of branch points in some of the radial burst networks, is due to resistive losses caused by concentrating more current down fewer links. The networks being optimised had no way to reduce the inherent resistance of the links after shortening them, such as by increasing strength, which would have offset these losses. This suggests that the ecological and coupled socio-ecological systems utilise multiple degrees of freedom to optimise networks to increase energetic consumption and/or reduce energetic loss, and that the optimal network as guided by natural selection is dependent on the different weights that the system associates with the energetic cost of link construction, maintenance, and resistance-driven loss.

Although the work here met the aims of developing and testing a spatially-explicit, thermodynamically-accurate methodology for modelling RADE networks, and applied it successfully to a proof-of-concept, this raises even more areas for exploration. Beyond improvements to the underlying model to incorporate additional degrees of freedom, such as link strength, and application of it to other case studies of specific RADE networks, there are several areas of future work that would be particularly instructive:

1. Multi-vector analysis: the increasing incorporation of distributed, heterogenous energy sources such as renewables, and the interconnection of networks involving multiple resource types, demands a methodology of analysing the interactions, resilience, and throughputs of these systems, and their impacts on the surrounding environment. A consistent one has yet to be applied (Mancarella et. al. 2016). The resource flow methodology here could be applied to analyse

nested and/or interconnected networks of multiple types of resources, providing a framework for better quantifying their energetic costs and capabilities.

2. Prediction of system complexity and other characteristics: as systems grow and incorporate more resources, and those of different types, they also increase in complexity. While different measures for spatial and temporal complexity have been put forward (Parrott, 2010), there is not yet a set framework for quantifying or predicting the complexity of a system. By generating networks with different constraints, costs, and underlying distributions of resources, different measures for complexity could be applied and evaluated. Possible networks could also be generated for known conditions, similar to the *A. mellifera* case study done here, and analysed for complexity, resilience, equity, and sustainability, providing insight into the interplay between those characteristics and physical network attributes.
3. Information: as discussed earlier, and clearly demonstrated in the case of bees, information creates a ‘soft structure’ between components of a decentralised network, allowing it to operate as a unified whole. Developing a methodology to explicitly incorporate and quantify the stocks and flows of information within networks, along with the information contained within the physical structures, would allow for more comprehensive and accurate systems modelling, as well as a better understanding of the impact of information within RADE networks.
4. Principles of generalised resource consumption and distribution: besides the seemingly ubiquitous sublinear scaling put forth in MTE, other generalised principles for energy consumption and entropy production exist, such as the Maximum Entropy Production principle (MEP), which states that systems evolve toward states of higher entropy production (Kleidon et. al., 2010). By testing these laws in a generalised resource flow network, such as the ones initially used to test the modified resource flow methodology, without the constraints of specific models, their universality can be more accurately determined, along with any conditions that may cause deviations from the observed phenomena on which the proposed law is based.

The ubiquity of resource acquisition, distribution, and end-use networks, their similarities across diverse systems, and their impacts on the systems they support and are nested within, make them both important and fascinating to study from theoretical and practical angles. As shown here, there is much more to be done in improving and applying methodology for their modelling and analysis, but the work presented is a new direction in doing so that shows great potential.

6. References

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7. Appendix A: Nectar Resources

Table 7. Nectar resources. This table shows the relevant data for the twenty-five melliferous species used to generate the five resource distribution maps in the HiveNetGA optimisation. The resource distribution maps were grassland (G), grassland farmland (GF), grassland park (GP), grassland woodland (GW), and woodland (W), with some species used in multiple maps if appropriate (i.e. a species listed in woodland could also appear in the woodland sections of the grassland woodland map). If the precise nectar sugar concentration for the species could not be found, that of a closely related species was used, as shown by an asterisk (*) in the data source column.

Species	Scientific Name	Vegetative area of habitat (%)	Habitat	Nectar sugar concentration (mg mg^{-1})	Voltage (J mg^{-1})	Nectar sugar concentration data source
Apple tree	<i>M. domestica</i>	2.70	W	0.50	8.60	Scullen & Vansell, 1942
Apple tree	<i>M. domestica</i>	15.14	GF	0.50	8.60	Scullen & Vansell, 1942
Blue bugle	<i>A. reptans</i>	0.09	G	0.30	5.16	Macukanovic-Jocic et. al., 2004
Bluebell	<i>H. non-scripta</i>	1.45	G	0.35	6.02	O'Rourke et. al., 2014
Bluebell	<i>H. non-scripta</i>	21.11	GW	0.35	6.02	O'Rourke et. al., 2014
Buttercup	<i>R. bulbosus</i>	0.87	F	0.15	2.58	Fornoff et. al., 2017*
Buttercup	<i>R. bulbosus</i>	2.04	GP	0.15	2.58	Fornoff et. al., 2017*
Cherry tree	<i>P. avium</i>	1.60	G	0.30	5.16	Gyan & Woodell, 1987
Cherry tree	<i>P. avium</i>	4.48	W	0.30	5.16	Gyan & Woodell, 1987
Common dogwood	<i>C. sanguinea</i>	1.52	G	0.25	4.30	Farkas & Zajacz, 2007
Common groundsel	<i>S. vulgaris</i>	0.15	G	0.47	8.08	Vanparrys et. al., 2011*

(Continued)

Species	Scientific Name	Vegetative area of habitat (%)	Habitat	Nectar sugar concentration (mg mg⁻¹)	Voltage (J mg⁻¹)	Nectar sugar concentration data source
Common groundsel	<i>S. vulgaris</i>	0.96	GP	0.47	8.08	Vanparys et. al., 2011*
Creeping Thistle	<i>C. arvense</i>	5.09	G	0.56	9.63	Tartaglia & Handel, 2014
Creeping Thistle	<i>C. arvense</i>	2.37	W	0.56	9.63	Tartaglia & Handel, 2014
Dandelion	<i>T. agg.</i>	2.15	W	0.20	3.44	Hicks et. al., 2016
Field maple	<i>A. campestre</i>	3.38	G	0.52	8.94	Scullen & Vansell, 1942
Field mustard	<i>S. arvensis</i>	0.80	GP	0.23	3.96	Masierowska, 2003
Geranium	<i>G. dissectum</i>	0.85	G	0.36	6.19	Masierowska, 2012
Geranium	<i>G. molle</i>	0.68	GP	0.36	6.19	Masierowska, 2012
Geranium	<i>G. molle</i>	6.56	GP	0.36	6.19	Masierowska, 2012)
Ground ivy	<i>G. hederacea</i>	1.27	W	0.20	3.44	Kulloli et. al., 2011*
Hawthorn	<i>C. monogyna</i>	7.19	GP	0.50	8.60	Gyan & Woodell, 1987
Hawthorn	<i>C. monogyna</i>	15.14	GP	0.50	8.60	Gyan & Woodell, 1987
Hogweed	<i>H. sphondylium</i>	0.94	G	0.18	3.10	Fornoff et. al., 2017
Horse chestnut	<i>A. hippocastanum</i>	5.16	G	0.74	12.73	Percival, 2013, pg. 89
Horse chestnut	<i>A. hippocastanum</i>	3.38	GP	0.74	12.73	Percival, 2013, pg. 89
Iris	<i>L. galeobdolon</i>	3.56	W	0.20	3.44	Wesselingh & Arnold, 1999

(Continued)

Species	Scientific Name	Vegetative area of habitat (%)	Habitat	Nectar sugar concentration (mg mg⁻¹)	Voltage (J mg⁻¹)	Nectar sugar concentration data source
Lady's Smock	<i>C. pratensis</i>	0.23	G	0.50	8.60	Percival, 2013, pg. 89*
Oilseed rape	<i>B. rapa</i>	1.36	F	0.51	8.69	Percival, 2013, pg. 89
Oilseed rape	<i>B. rapa</i>	2.02	GW	0.51	8.69	Percival, 2013, pg. 89
Onion	<i>A. cepa</i>	1.84	F	0.50	8.60	Farkas et. al., 2012
Spear thistle	<i>C. vulgare</i>	0.62	GP	0.56	9.63	Tartaglia & Handel, 2014
Spear thistle	<i>C. vulgare</i>	0.62	W	0.56	9.63	Tartaglia & Handel, 2014
Sweet chestnut	<i>C. sativa</i>	15.14	GW	0.22	3.78	Gulácsy, 1975 (cited in Farkas & Zajacz, 2007)
Sweet chestnut	<i>C. sativa</i>	4.48	W	0.22	3.78	Gulácsy, 1975 (cited in Farkas & Zajacz, 2007)
Sycamore maple	<i>A. pseudoplatanus</i>	10.42	W	0.52	8.94	Scullen & Vansell, 1942
Wild Angelica	<i>A. sylvestris</i>	2.93	G	0.22	3.78	Stpiczyńska et. al., 2015
Yellow archangel	<i>L. galeobdolon</i>	2.69	W	0.20	3.44	Macukanovic-Jocic et. al., 2004

8. Appendix B: Breeder Parameterisation Tests

Table 8. Breeder parameterisation tests for single criterion cost functions. Yellow highlighting shows which parameter(s) were being tested as compared to the initial run in the first row, and blue shading shows parameterisation chosen for use. Test runs with power marked as NA did not complete as the optimisation reached a point where it did not have any valid networks to use for breeding the next generation. The probability of mutation is much lower as these tests were performed before the mutation operator was changed so it could not remove links, so the mutation probability shown is for the first round of single criterion optimisations only. The breeder tests for multi-criteria cost functions used the revised mutation operator, so the selected higher mutation value from these tests was applied to the second round of single criterion cost function optimisations as well.

Population size	Number of best networks kept	Number of worst network removed	Initial probability of local search	Final probability of perturbation	Probability of mutation	Result: Power ($J \text{ sec}^{-1}$)
1000	12	12	0.2	0.01	0.05**	139.925
1500	18	18	0.2	0.01	0.05	135.263
1000	10	10	0.2	0.01	0.05	136.887
1000	5	12	0.2	0.01	0.05	133.166
1000	12	5	0.2	0.01	0.05	NA
1000	12	12	0.25	0.01	0.05	136.312
1000	12	12	0.2	0.01	0.015	138.212
1000	12	12	0.15	0.01	0.05	NA
1000	12	12	0.2	0.01	0.0015	137.434
1000	12	12	0.2	0.001	0.05	135.523
1000	12	12	0.2	0.05	0.05	138.209

Table 9. Breeder parameterisation tests for multi-criteria cost functions. Yellow highlighting shows which parameter(s) were being tested as compared to the initial run in the first row, and blue shading shows which parameterisation was chosen for use. Since the initial probability of connection was closely related to the link length and amount of disconnection explored in the solution space, both multi-criteria cost functions were run with two values (0.5 and 0.75) over each resource distribution map. Some parameters that were tested for the single criterion parameterisation (Table 8) were reused in the multi-criteria optimisations, to reduce the number of test runs. Performance validation showed the success of the parameterisation at encouraging a thorough exploration of the solution space.

Population size	Initial probability of local search	Final probability of local search	Probability of mutation	Initial probability of connection	Size, summary of Pareto front
1200	0.3	1	0.1	0.75	3007 networks. Thorough coverage of range of values for each cost.
1200	0.3	1	0.1	0.5	191 networks. Significantly less coverage of link length for each level of power flow, resource type disconnection
1200	0.2	1	0.1	0.75	2054 networks. More coverage of link length and power consumption than baseline, less coverage of resource disconnection
1200	0.3	1	0.2	0.75	946 networks. Hardly any coverage of link cost.
1200	0.2	1	0.2	0.75	5416 networks. Good coverage of power consumption and resource disconnection, adequate coverage of link length
1200	0.2	1	0.1	0.66	2782 networks. Limited coverage of each cost.
1200	0.3	1	0.1	0.66	5759 networks. No coverage of link length.
1500	0.3	1	0.1	0.75	2463 networks. More coverage of link length and resource flow than baseline.
1000	0.3	1	0.1	0.75	2382 networks. Limited coverage of link length and power consumption.
1200	0.25	1	0.15	0.75	2617 networks. Very limited coverage of link cost, resource disconnection.

9. Appendix C: Glossary

Due to the multidisciplinary approach taken in this thesis, the terminology spans ecology, physical science, engineering, computer science, network and complexity science, and apiology (the study of bees). As some of these terms may not be familiar to practitioners of those subjects individually, or may be used in a different context in the work presented, they have been defined here with respect to how they are used in this thesis. Terms are organised alphabetically within each subject heading.

Apiology

Crop: the specialised pouch in the abdomen of honey bees, used for transporting nectar from flowers to the hive (Seeley, 1995).

Melliferous species: A species that secretes nectar used by bees to create honey. Not all nectar-secreting plants are melliferous, while others are especially so (Masierowska, 2003).

Waggle dance: A pattern of movement that a forager utilises to direct other foragers to particularly good nectar sources. By repeating different turning and running movements, the forager conveys both distance and direction to onlooking foragers who do not have a floral patch that they are currently exploiting (Seeley, 1995).

Computer Science

Agent: Typically, an individual unit within a system, which represents a social actor with a level of control over themselves and aspects of their environment (Gilbert, 2008). In this work, refers to a node in the network that demands and consumes resources, as opposed to supplying them.

Agent-based model: A modelling framework in which individual components are modelled as ‘agents’, each with internal rules governing their behaviour and interactions with other agents and their environment (Gilbert, 2008). Example: a model of a colony of ants, foraging for food and bringing it back to the anthill.

Annealing: A process by which parameters are slowly ‘cooled’ or lowered, similar to the process of annealing in metalworking, to reduce the likelihood of significant changes to a solution or the acceptance of a less-fit solution. Acts to transition the optimisation from global to local search. Commonly used in an optimisation algorithm called ‘simulated annealing’ (Gandomkar et. al., 2005), but can be used within other algorithms too, as was done here.

Branch point: A node in the network that does not supply or demand resource, but instead is a neutral junction between two or more links. Used as an additional degree of freedom when exploring different network topologies.

Chromosome: A possible solution for the optimisation problem being solved by the genetic algorithm (Goldberg, 1989).

Combinatorial explosion: A characteristic of some optimisation problems, where the problem involves multiple variables or degrees of freedom that be combined in so many possible configurations as to be unsolvable by traditional methods, such as brute-force solving and evaluating (Klamt & Stelling, 2002).

Crossover (single point, multi-point, uniform): A genetic operator used to simulate genetic recombination, by combining the genes of two ‘parent’ chromosomes, to produce two new ‘offspring’ chromosomes. This combining can occur at a single point along the chromosome (single-point crossover), multiple points (multi-point crossover) or at each gene with an equal probability (uniform crossover) (De Jong & Spears, 1992).

Elitism: preserving the best network or networks from one generation to another, without applying genetic operators (Goldberg, 1989).

Evolutionary algorithm: A class of optimisation algorithms that uses operators designed around principles of evolution and genetic recombination to improve a set of solutions (Holland, 1975).

Fitness function: a cost function where the objective is to maximise each of the criterion as opposed to minimise them (Goldberg, 1989).

Gene: A single characteristic or data point of a solution, or chromosome, evaluated by the genetic algorithm (Goldberg, 1989).

Genetic algorithm (GA): An evolutionary optimisation algorithm that uses computational operators designed to reflect processes of genetic recombination and mutation on a population of solutions, to perform a search of the entire possible solution space (Goldberg, 1989).

Generation: A single iteration of the main loop of a genetic algorithm, involving evaluating and ranking a population, and generating a new population for breeding (Goldberg, 1989).

Genetic operator: A computational function applied to a chromosome or pair of chromosomes to alter or recombine them in a manner reminiscent of evolutionary processes, such as genetic recombination or mutation (Goldberg, 1989).

Global search: A search strategy by which the whole solution space is searched to identify the global optimum, or best possible solution, as opposed to a local optimum, or improvement of the current solution (Balaprakash et. al., 2012).

Local search: A search strategy that focusses on the neighbourhood of a known good solution or solutions, via small changes in order to try to improve them. Can also be thought of as ‘exploiting’ known promising areas of the solution space (Balaprakash et. al., 2012).

Multi-criteria cost function: An objective guiding the optimisation that each solution is tested against for evaluation, that is comprised of multiple, potentially conflicting criteria to minimise. Results in a Pareto front of incomparable best solutions, where each solution is better performing in some aspect than its neighbours, but worse in others. Example: simultaneously minimise cost while minimising disruptions or failures (Fonseca & Fleming, 1993).

Mutation: A genetic operator wherein each gene within the chromosome is mutated to a new value within the bounds of all possible values for that gene (Goldberg, 1989).

Niching/niche clearing: The process of subdividing a population of chromosomes into niches based on similar performance, within a certain threshold or ‘radius’, on each criterion in a multi-criteria cost function, then removing the chromosomes from each niche that are in excess the set niche ‘capacity’ (Horn et. al., 1994; Pétrowski, 1996).

Node: Used in this work as a generic term for an element in the network, typically acting as a point of supply or demand. This definition is more aligned with the network science definition of node (a component in a network (Barabási, 2016)), as opposed to the electrical engineering definition of node (a junction between two elements, or branches (Glover et. al., 2012)).

Offspring networks: New networks produced via crossover, mutation, perturbation, cloning, or some combination thereof of networks in the previous generation (Goldberg, 1989).

Pareto dominance: A solution that performs equally or better than another solution on all criteria, and is better than the other solution on at least one criterion (Fonseca & Fleming, 1993).

Parallel search: A search strategy in which multiple possible solutions are explored simultaneously (Hamblin, 2013).

Perturbation: A genetic operator that perturbs each evolvable characteristic or gene within a solution or chromosome, within a certain variance of the original value. Not a classic genetic algorithm operator found in the literature; developed for the purposes of the work presented here.

Population: The total collection of possible solutions, or chromosomes, being evaluated by the genetic algorithm in a given generation, or round (Goldberg, 1989).

Premature convergence: When an optimisation algorithm converges too quickly on a local optimum, as opposed to searching the entire solution space to find the global optimum (Goldberg, 1989).

Roulette wheel selection: A process of selecting the breeding population, where the cumulative distribution function of the fitness of the population is sampled randomly, with or without replacement (Goldberg, 1989).

Single criterion cost function: A single objective or criterion guiding the optimisation that each solution is tested against for evaluation, resulting in a single best solution identified for each generation (Goldberg, 1989). Example: minimise total travel time.

Solution space: Also known as feasible region. All points which satisfy the constraining conditions of an optimisation (Zhou et. al., 2011).

Stochastic universal sampling: A method used for selecting individuals from the current generation to be used in creating the next generation, via sampling a cumulative distribution of the fitness of the current population at equally-spaced intervals (Baker, 1987).

Tournament selection: A process of selecting the breeding population to create the next generation of possible solutions to an optimisation problem, in which chromosomes are compared in a pairwise manner, with the better-performing chromosomes being used to create the breeding population and therefore the next generation (Baker, 1987).

Truncation: Removing the worst network or networks from a generation, before selecting the breeding population (Baker, 1987).

Ecology

Circuit Theory: A methodology based on nodal analysis (see Engineering: Nodal analysis) that is used to evaluate the probabilities and difficulties with which a random walker, such as an organism, will pass through a habitat corridor (Gimona et. al., 2012).

Coupled socio-ecological system: A system comprised of both natural and human or human-engineered components, with a high degree of interconnection and interdependency (Berkes & Folke, 1998, cited in Polhill et. al., 2015). Examples: natural resource extraction, transportation, and use networks, where the resources are mined or collected from ecosystems and transported across them, significantly impacting and being impacted by those systems.

Energetics: The study of energy transformation (Lehnninger, 1973), used here to mean specifically the energy used in and/or gained from a process, such as resource acquisition and distribution.

Generic focal species: A theoretical species used in modelling to represent a group of species of interest for whom complete data is not available. The needs and characteristics of the focal species are those likely to be similar to the species that they are used to represent (Watts et. al., 2010).

Interactional/interaction-based model: An ecosystem model that focusses on the interactions between species, as opposed to the spatial distances (Jørgensen, 2008). Example: a food web.

Metabolic Theory of Ecology (MTE): A theory centred on Kleiber's law of allometric scaling, which posits that the metabolic rate of organisms is the central rate governing all ecological process and pattern (Brown et. al., 2004).

Optimal Foraging Theory (OFT): A theory used to predict the behaviour of an animal while foraging or hunting for food. The theory posits that natural selection favours behaviours that maximise energy consumption, such that in foraging, the animal chooses a strategy that maximise a certain currency, such as rate or efficiency of energy consumption, within the constraints of its environment (Pyke, 1984).

Superorganism: A collection of organisms whose group function has properties analogous to those of individual organisms (Wilson & Sober, 1989). The term has also been applied to abiotic systems with constituent subparts that work together to create a unified whole with emergent properties (Odum, 1966). Example: eusocial insects, such as bees or ants; human society.

Engineering

Alternating Current (AC): Current flow which periodically changes direction as a result of voltage reversing (Overbye et. al., 2004).

Admittance: The ease with which current passes through a link or branch – the reciprocal of impedance. Takes into account both conductance and susceptance. Applicable only to AC power flow (Glover et. al., 2012).

Conductance: The inverse of resistance. A measure of the ease with which current passes through a conductor. Applicable to both AC and DC power flow (Glover et. al., 2012).

Current: A measure of the rate of flow of charged particles. Measured in amps (A, coulombs sec⁻¹) (Glover et. al., 2012).

Direct Current (DC): Unidirectional current flow (Overbye et. al., 2004).

Electrical analogue: the representative component in an electrical system for a component in a non-electrical system, or the entire electrical system made up of representative components from a non-electrical system (Odum, 1971). Examples: voltage as the electrical analogue of the sugar concentration of a resource, a circuit of voltage sources and resistors as the electrical analogue of an ecosystem.

Ground: A reference point from which other voltages in a circuit are measured (Calahan et. al., 1974).

Impedance: the difficulty presented to a flow of current along a line – the reciprocal of admittance. Takes into account both resistance and reactance. Applicable only to AC power flow (Glover et. al., 2012).

Linear circuit: A circuit in which the output is a linear function of the inputs, as the inputs and outputs are in the same sinusoidal frequency (Zumbahlen, 2008).

Load flow analysis: A methodology for calculating the steady-state power flow in an AC electric grid (Glover et. al., 2012).

Lossless lines: An assumption that the losses along branches or lines in a power grid due to resistance are negligible enough to be ignored, as the reactance-driven losses are much higher. Used when adapting the AC power load flow analysis methodology for DC power (Overbye et. al., 2004).

(Modified) nodal analysis: A technique for calculating the voltages at each node in a circuit. Modified nodal analysis also determines some branch currents (Ho et. al., 1975).

Newton-Raphson method: A method of solving a system of equations by iteratively solving and updating a Jacobian matrix (Glover et. al., 2012).

Power: A measure of the rate of doing work, or energy transfer per unit time. Measured in Watts (W, Joules sec⁻¹) (Glover et. al., 2012).

Resistance: The measure of the difficulty experienced by a steady-state flow of current when passing through a conductor such as a wire. Applicable to both AC and DC power flow. Measured in Ohms (Ω). (Glover et. al., 2012).

Susceptance: The imaginary part of admittance: the ease with which a change of current passes through a conductor. Applicable only to AC power flow (Glover et. al., 2012).

Voltage angle: the difference between the voltage phase angle of a current-sending and current-receiving bus. Applicable only to AC power flow (Glover et. al., 2012).

Voltage (magnitude): the quantity of voltage entering or leaving a node, such as a generator or load bus. Applicable to both AC and DC power flow (Glover et. al., 2012).

Network and Complexity Science

All paths: A method of identifying all paths between any two nodes in a network (Carmi et. al., 2008).

Complex adaptive system: A system displaying emergent properties, or behaviour that is more than the sum of actions by its constituent parts, that is also anticipatory of and evolving in response to changes in its surrounding environment (Holland, 1992).

Complexity: A characteristic of being comprised of multiple components, whose interactions cause the system to display emergent properties and behaviours that are not displayed by any one of the individuals (Holland, 1992).

Emergent property: A property of a system or whole that is not contained within any or all of its constituent parts, but rather arises from the interaction between them (Holland,

1992). Example: branching networks that result from the interaction between balancing multiple, conflicting criteria of maximising resource consumption whilst minimising energetic cost.

Fractal/hierarchical branching: A structure that is self-similar, where the whole has the shape of one or more of the parts, across several scales (Brown et. al., 2002). Examples: snowflake, vascular system, fern.

Hebbian learning: A process by which the repeated firing of one neuron by another causes the second neuron to become more sensitive to the firing of the first through stronger links between the two, i.e. the efficiency of the first neuron at firing the second is increased (Schoenharl, 2005).

Information: the values of characteristics of a process' output, which informs about the process and its inputs (Losee, 1997). In the context of RADE networks, the existence of the infrastructure is itself information about the process of creating it and the materials and/or energy utilised, and information from the process of extracting, distributing, and using the resource itself is fed back into the network to improve it.

Infrastructure: The structures used to comprise a system, as they exist in space and/or time. Used mostly to refer to network infrastructure in this work, or the structures that form the energy carriers, links, and nodes in the network. Represents the embodiment of energy investment in material structures (Jarvis, 2018). Examples: tree branches, pipelines, veins, flight paths, bees.

Least-cost path/shortest path: A method of identifying the path between two nodes in a network that is the shortest, or contains the fewest links, and/or path with the least total cost, if weighted, between any two nodes (Barabási, 2016).

Node degree: The number of connections, or links, that are attached to a given node (Barabási, 2016).

Radial burst network: A network topology characterised by a node or cluster located centrally, with unique links connecting directly to distributed resources (Banavar et. al., 2010).

Random network: A network where the degrees of the nodes are a uniform distribution (Barabási, 2016).

Scale-free network: A network where the degrees of the nodes are a power-law distribution, with some nodes having a very high degree, and most having a very low degree (Barabási, 2016).

Self-organisation: A process of order and structuring within a system arising from decentralised interactions of components. A feature of complex adaptive systems (Holland, 1992).

Stylised network: A theoretical network, designed for analysing network properties and dynamics, but not necessarily modelled after a real-world network.

Topology: the layout of nodes and links within a network, or the dimensionality of the underlying space that the network fills. Example: radial burst topology, three-dimensional plane topology.

Physical Sciences

(Energetic) efficiency: The ratio of useful energy consumed per unit of energy produced (Odum & Pinkerton, 1955).

Entropy: The number of microscopic configurations of a system that can produce a given macroscopic configuration. A highly organised, ordered system has a very low entropy, because there are very few microscopic configurations of particles that correspond to that macroscopic state. In contrast, there are infinitely more microscopic configurations that correspond to a state of thermodynamic equilibrium, or maximum entropy (Kleidon, 2016).

First law of thermodynamics: the conservation law, stating that energy cannot be created or destroyed, such that the total energy of a closed system is constant (Kleidon, 2016).

Free energy: The amount of energy available to a system to perform work, after taking into account losses due to entropy (Kleidon, 2016).

Second law of thermodynamics: states that entropy in a closed system not yet at thermodynamic equilibrium cannot decrease, and entropy increases during energy conversions, such that the overall state of the system evolves toward thermodynamic equilibrium (Kleidon, 2016).

Thermodynamic equilibrium: A state of maximum entropy, in which no further net energy transformations or exchanges can take place (Kleidon, 2016).

Thermodynamically open system: A system that is able to exchange energy, entropy, and mass across its boundaries (Kleidon, 2016). Examples: the earth system, an organism's body.

Resource Distribution

Acquisition: The process of extracting a resource from its original location (Jarvis et. al., 2015). Examples: mining, foraging.

Distribution: The process of moving resources from points of origin to points of demand and/or use (Jarvis et. al., 2015). Examples: rail transport of coal, water flowing through pipes.

End use: The process of resources being consumed to produce outputs deemed useful (Jarvis et. al., 2015). Examples: natural gas being used to heat a home.

Multi-vector energy analysis: Analysis of a system of multiple, heterogenous energy inputs (Carradore & Turri, 2009). Example: a distributed system of solar panels, wind turbines, and hydropower stations.

Primary energy: Energy as initially extracted from natural sources (De Stercke, 2014). Examples: sunlight, crude oil, coal.

Resource Acquisition, Distribution, and End Use (RADE) network: A network of points of resource supply and demand, or end use, linked by resource transportation systems such as roads, canals, railways, or forager movements and paths (Jarvis et. al., 2015).