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Modelling nutritional interactions: from individuals to communities

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Nutrient acquisition is a major context for ecological interactions among species but ecologists and nutritionists have developed theory in isolation from each other. Developments in agent-based modelling, state–space modelling of nutrition and multi-scale modelling of landscape ecology provide the components for a new synthesis in nutritional ecology linking the nutritional biology of individual organisms to population- and community-level processes across multiple scales within an evolutionary context. We review the core elements for such a synthesis and set out the principles for a generic modelling framework that could be used to test specific ecological hypotheses.

Introduction

In recent years there have been calls to bridge the divide between the functional study of individual organisms and community ecology with the aim of deriving general principles of community structure, function and evolution from the physiology and behaviour of individuals [1–4]. Indeed, there can be few more important challenges in modern biology than explaining how the features of organisms contribute to the populations, communities and ecosystems within which they exist and how these in turn respond to changing environmental conditions.

Pre-eminent among the interactions between organisms are those involving the search for nutrients: herbivores eat plants and in turn might induce defensive chemical responses, predators eat prey and sometimes conspecifics attack and eat each other. As a consequence, individuals prosper or not, populations grow or decline, trophic inter-actions arise, communities change and ecosystem dynamics appear. The challenge remains to develop models that take account of an individual organism's simultaneous membership of a group, population, community and ecosystem, in other words, a heterarchical modelling framework for nutritional ecology [5].

Here we first consider the general criteria for such a synthesis and the available modelling approaches that might achieve it. Next we identify and review the component parts for development of a new synthesis in nutritional ecology before providing an example of what such a synthesis might look like.

Glossary

Agent-based models: also known as individual-based simulation models, in which simulated agents that follow local interaction rules are used to explore and generate complex patterns at larger scales.
Allometric scaling exponent: metabolic rate and other physiological variables scale with body mass in the form of power laws with exponents that seem to be multiples of 0.25 [32].
Biophysical ecology: applies the principles of heat and mass transfer to calculate how environmental conditions interact with body size, physiology and behaviour to affect the performance and distribution of organisms [65].
Dynamic energy and mass budget model: uses surface area and volume relationships, together with 'synthesizing units', to model nutrient and energy acquisition and allocation, partitioning the organism into structural body mass and reserves [36].
Food aversion learning: a form of associative learning in which an animal associates sensory cues from a food with some deleterious consequence of eating that food and subsequently avoids the food.
Geometric framework: state–space geometric models of nutrition that facilitate identification and quantification of salient resources, organismal traits and their interactions [21].
Growth target: the optimal amount and blend of ingested nutrients for allocation to somatic and reproductive growth and storage [21].
Heterarchical models: models that take account of an individual organism's simultaneous membership of a group, population, community and ecosystem.
Indirect interactions: interactions between two species that are mediated by other species rather than by direct interactions.
Intake target: the amount and blend of nutrients, which, if ingested over a given period, will maximize an organism's fitness [21].
Lévy flight: a type of random walk pattern in which the step lengths come from a distribution with a heavy power-law tail, producing sequences of short movements separated by infrequent long steps.
Nutritional rail: a vector in a multidimensional nutrient (or other food component) space representing the composition of a food containing a fixed proportion of nutrients and other components [21].
Plant secondary metabolite (PSM): molecules produced by plants, the presence of which is often characteristic of particular plant taxa and which seem not to be directly involved in primary metabolism.

Modelling nutritional interactions

It has recently [5] been argued that models of nutritional ecology need to meet three criteria. First, they must be *nutritionally explicit*, focusing on the acquisition and use of multiple nutrients rather than emphasising single food properties such as energy or toxins or using chemical elements that do not correspond to regulated molecular complexes as currencies. Second, they must be *organismally explicit*, considering functional consequences and mechanistic constraints of nutritional decisions at the level of the individual. Third, they need to be *ecologically explicit*, capable of being used at several interacting levels from individuals to populations to communities. In addition, given the importance in ecology of dynamics in time and space, nutritional models that are *dynamic and spatially explicit* will provide a bridge between nutritional and community ecology [5].

Modelling nutritional interactions in a manner that integrates these essential criteria has become more achievable with recent advances in three research disciplines (Figure 1): (a) agent-based modelling (ABM; also known as individual-based models) whereby interacting individuals following simple local rules can generate complex patterns at larger scales [6–9]; (b) state–space geometric models of nutrition that facilitate the identification and quantification of salient resources, organismal traits and their interactions [10,11]; and (c) models to represent environments across multiple spatial and temporal scales [12–14] with which simulated agents can interact *in silico* [15–17].

These three fields have yet to be integrated within a single modelling platform. Hence, although encouraging efforts have been made to use ABMs to explore patterns of resource use in foraging animals [9,18,19], these models are not yet nutritionally explicit because they do not take account of the multiple nutrient dimensions that have been shown to determine the foraging behaviour of a taxonomically diverse range of herbivores, omnivores and carnivores [10,20–22]. By contrast, whereas nutritionally explicit state–space models have recently been proposed [11,23] and used to begin to explain ecological interactions such as niche partitioning [24], animal migration [25] and limits on the number of trophic levels [5], they have yet to be used in the context of dynamic, spatially explicit models of nutritional environments.

Achieving nutritional explicitness: the geometric framework

When modelling foraging animals, it is essential to capture not only the multidimensional nature of nutritional requirements, but also the relative values of foods in relation to these requirements, the behavioural and post-ingestive responses of animals when feeding on diets of varying chemical composition, and the growth and performance consequences of being restricted to particular dietary regimes.

The geometric framework (GF) is a state–space approach developed for this purpose [10,11]. In the GF, the current nutritional and growth states of an animal are represented as moving points in multidimensional nutrient space, changing over time with intake, metabolism, growth, reproduction and excretion. Optimal (target) states for growth, intake and metabolism are represented in the same space. Foods are represented as vectors determined by the balance of the relevant components each food contains (nutritional rails). By eating, the animal changes its nutritional state along the vector of the chosen food rail. A nutritionally imbalanced diet forces the animal into a compromise between over-ingestion of some food components and under-ingestion of others relative to requirements, with associated costs. The animal can achieve its
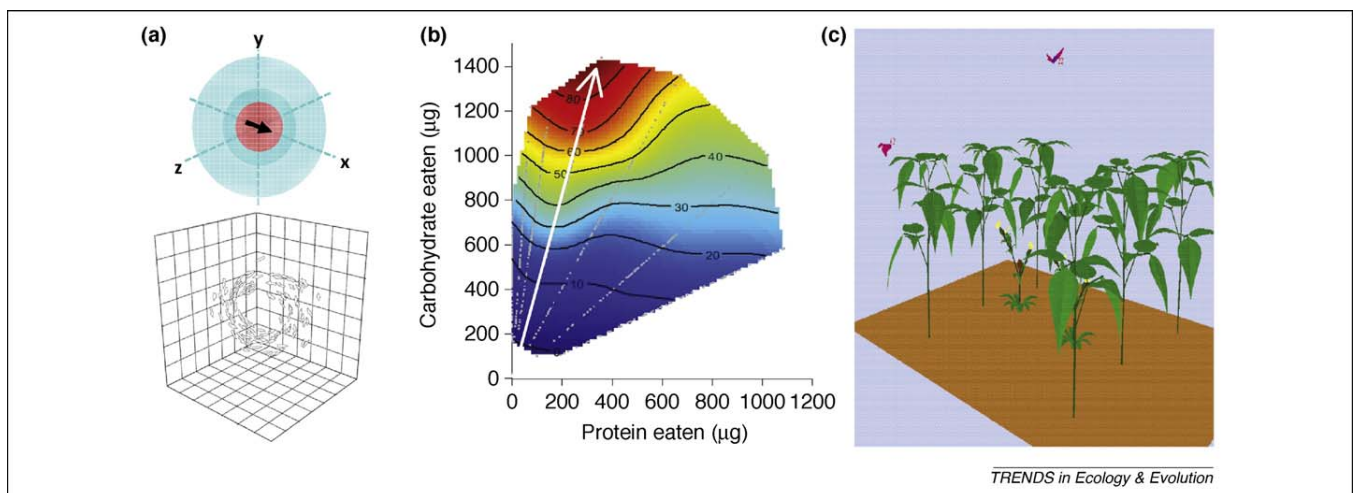
Figure 1. Three modelling approaches potentially relevant to the development of a new synthesis for nutritional ecology. (a) Agent-based models of collective behaviour (after [79]). Small adjustments of local interaction rules between agents, such as zones of attraction (light blue), orientation (darker blue) and repulsion (pink), result in substantial changes in the behaviour of moving groups, leading to production of cohesive aggregations, aligned swarms or (as shown) circular mills of moving agents. (b) State–space models of nutrition, the geometric framework, in which regulation of nutrient intake and allocation is represented in multidimensional nutrient space and related to performance response surfaces. The example shows a surface for lifetime egg production (LEP) in *Drosophila* mapped onto intake of protein and carbohydrate derived by confining flies to one of 28 diets [49]. When flies were allowed to select between complementary foods they regulated their intake of protein and carbohydrate to maximize LEP (white arrow). (c) Landscape models, represented here by an example of an L-Systems plant growth model, with simulation of butterfly foraging. Virtual weeds, which provide a source of nectar for the virtual butterflies, are interspersed in a planting of bean plants modelled from measured plants. Movement is random unless the level of carbohydrate in the gut reaches zero, in which case the butterflies move to the nearest flower to feed. Young bean leaves attract butterflies in an egg-laying state (courtesy of Glaze, Hanan and Zalucki, from whom the dynamic simulation output can be obtained; contact: j.hanan@uq.edu.au).

intake target if it mixes its diet with a food containing a complementary imbalance of nutrients. When nutritionally balanced or complementary foods are unavailable, the animal cannot balance its nutrient intake but can achieve its growth target by selectively excreting ingested excesses. The challenge is for the animal to arrive at a balance between over- and under-ingestion that minimizes fitness costs.

Experimental evidence from a range of taxa across multiple feeding guilds indicates that protein and non-protein energy (carbohydrate and/or fat) dominate ingestive behaviour, with specific systems regulating the intake of each [11,20,21]. Micro-nutritional components of food are either ingested in adequate amounts as a by-product of food mixing to achieve macronutrient regulation or else are selectively ingested from near-pure sources when in deficit (e.g. sodium [26]). Hence, for many purposes, models structured around two macronutrient dimensions will capture most of the important nutritional responses in individual foragers. Importantly, the approach is readily extendable to other nutrients simply by adding additional axes in nutritional space.

Non-nutritional food components

Non-nutrient components of food, such as plant secondary metabolites (PSMs), indigestible bulk, silica (grasses) and calcium carbonate (algae), play important roles in food selection, ingestion and utilization by consumers [27–29]. The generality of the GF is such that dimensions can represent *any* food component. The distinction between toxins and nutrients, for example, is not always clear-cut: nutrients can be toxic at high levels and low doses of a toxin can be beneficial [30]. Both nutrients and non-nutrients can be accommodated as dimensions with differing intake target coordinates and costs, facilitating exploration and modelling of their pre- and post-ingestive influences and their interactive effects [31].

Achieving organismal explicitness: linking nutrition to other traits

In addition to its nutritional state, traits that mediate an organism's nutritional relations with its environment include its size, state of knowledge about the environment and its behaviour. These traits interact and ultimately determine an organism's fitness.

Size effects and metabolic scaling

The relationship between body mass and rate of energy expenditure can be captured using allometric scaling exponents [32], although such metabolic models are typically not organismally explicit, to the extent that they subsume the often complex relationships between body size and other traits such as gut size, specific nutrient requirements and diet composition [33–35]. Subsuming such complexity in the search for broad generality obscures a rich source of adaptive organismal traits. For example, metabolic rate can vary substantially within an individual and between species with diet composition as a result of facultative diet-induced thermogenesis, in which metabolic rate is enhanced as a regulatory response to burn-off of excess carbohydrate on energy-rich diets [34]. Dynamic energy and mass budget models [36] provide a promising alternative framework that mechanistically unites the processes of feeding, assimilation, metabolism, growth and reproduction as functions of surface areas and volumes.

Knowledge state

Three knowledge states are relevant to the behaviour of foragers: short term learning and memory; intermediate memory via parental effects; and ancestral memory embodied genetically in the default phenotype [37]. Hence, an animal is born with a set of default expectations, e.g. about which food types will be encountered. Learning from experience then enables the animal to assess the extent to which a food can supply its nutritional requirements now or in the future. Three types of nutritional-state-dependent learning have been reported for insects and vertebrates [38,39]: (a) learned positive associations (e.g. remembering food cues or locations that provided high-protein food); (b) learned aversions (e.g. avoiding cues or locations previously associated with toxic or nutritionally poor food); and (c) non-associative responses (e.g. move more or find novel foods attractive when in a state of deficit). Knowledge state can have a direct effect on the search strategy used by organisms. For example, in the absence of pertinent local information, individuals might be expected to use an efficient random search strategy (e.g. a Lévy flight [15,16]).

Linking nutritional state to behaviour: feeding

Nutritional state determines whether and how much of a given food is eaten. Such a relationship has been demonstrated experimentally for insects, in which nutritional regulatory behaviour results from blood-borne feedback that directly modulates the responsiveness of external taste receptors to specific nutrients in foods [38]. Hence, a locust that is protein-deprived but sugar-replete has specifically elevated gustatory responsiveness to amino acids in food and low responsiveness to sugars, and vice versa. Nutrient-specific regulation of food selection also occurs in vertebrates [21,40,41], albeit over longer time scales.

Likewise, non-nutrient food components modulate feeding behaviour in vertebrate and invertebrate herbivores. For example, mammalian herbivores modulate the size and frequency of meals to maintain blood concentrations of PSMs below toxic thresholds [42,43].

Linking nutritional state to behaviour: movement

If an animal is to achieve a balanced diet in a heterogeneous nutritional environment, the vector between current and optimal states in nutrient and PSM space needs to be linked to the probability of moving, the speed, direction and distance moved, and the probability and extent of turning [44,45]. Nutrient-specific effects on such locomotory variables have been quantified in both individuals and populations. For example, protein (but not carbohydrate) deprivation induces individual Mormon crickets to spend 50% more time walking, which increases the likelihood of an individual cricket encountering limiting high-protein resources [25]. When in a group, crickets are the most abundant source of protein and cannibalistic interactions

among protein-deprived insects drive mass movement [25]. Non-nutrients such as PSMs and other toxins also affect animal movement both directly and indirectly via their influence on nutritional state [46,47].

The relationship between nutritional and PSM state and locomotory behaviour determines the probability that an animal will stay on a nutritionally unbalanced food or leave it and has associated costs and benefits in a given environment. The costs of leaving might include subsequent failure to locate a better (or any) food, increased likelihood of encountering natural enemies and succumbing to inclement conditions [48]. Possible costs of remaining on an unbalanced food include eating too little of deficient nutrients and/or surpluses of others [11,29,49], missing better balanced foods located elsewhere, risks of inducing protective compounds in the host [50,51], depleting or degrading the resource and attracting natural enemies [52].

Linking nutritional state and behaviour to fitness

Arising from states, behaviours and their interactions are fitness outcomes, which are the basis for the evolution of new phenotypes. The GF has been used to quantify the performance consequences of ingesting deficits and excesses of nutrients and non-nutrient food components [11,49,53]. By experimentally measuring response surfaces over nutrient intake arrays (e.g. see Figure 1b) it is possible to quantify the performance consequences of being in a particular nutritional state and thus to explore the consequences of excesses and deficits in multiple nutrient dimensions on processes such as growth, longevity, reproductive success, immune responses and movement rates [49,53].

Achieving ecological explicitness

The ecological consequences of nutrition arise through direct and indirect interactions among organisms as mediated by environmental conditions.

Interactions among organisms

When encountering each other, organisms have the potential to alter the behaviour, state or condition, distribution or survival of other organisms both directly and through indirect interactions [1,54,55]. The most direct nutritional interaction of all is when one organism consumes another. The consequences of being eaten can extend across various time scales and include death and removal from the environment, reduction in size and changes in the chemical composition of remaining or regrown tissues, which might either reduce or improve the suitability of a resource for subsequent consumers [50,56].

Social interactions between individuals can structure collective behaviours, including group movement and nutritional decisions [57,58] and the acquisition of knowledge about the environment [8,36,58,59]. Such interactions have been explored using ABMs in which interaction rules as simple as local attraction, alignment and repulsion (see Figure 1a) can produce phase transitions in behaviour at the group level [7,8,60,61].

The fact that scaling up from individuals to groups produces sudden transitions in organization illustrates an important theme that is expected to apply throughout the hierarchy from individuals to ecosystems, namely that scaling up is not a simple linear progression in pattern or process [12,62]. As observed for the emergence of complex group behaviour as a result of local interactions among individuals [7,8,60,61], understanding of phase transitions in biological organization relies on quantifying and modelling the interactions between lower-level entities (individuals, groups, populations, species, guilds, trophic levels) and across scales and levels [62]. When considered from this perspective, evidence of a phase transition itself could provide a criterion for defining higher organizational levels.

Environmental interactions

Environments comprise abiotic and biotic components distributed in space and time over multiple scales [12,13,62,63]. Key abiotic features affecting nutritional interactions include gradients in light, temperature, relative humidity and the abundance and ratios of chemical elements within the soil or water, with regular and stochastic variations in abiotic conditions at different spatial and temporal scales. Fundamental metrics for describing nutritional environments include measures of resource abundance and distribution, as well as spatial and temporal autocorrelation of key resource qualities, including nutrients and secondary metabolites within foods.

Environmental temperature is a primary determinant of nutritional behaviour and physiology. The range of temperatures and microclimates and thus body temperatures experienced by an animal depends on its size, mobility and thermoregulatory behaviour [64,65]. Body temperature interacts with metabolic rate, water balance and nutritional and non-nutritional state across multiple time scales (physiological, developmental, trans-generational and evolutionary). Changes in the thermal environment alter metabolic and water loss rates and consequently the amount and blend of nutrients required and non-nutrients tolerated. For example, a decrease in ambient temperature results in an increase in carbohydrate or fat consumption by rats but no change in their protein intake [66]. Changes in temperature can also result in changed tolerance to PSMs [67].

Recent developments in the field of biophysical ecology have facilitated landscape-scale calculations of the temperature, energy and water relations of organisms as a function of abiotic (climate, topography, vegetation, soil) and biotic (behaviour, morphology and physiology) variables [65]. The spatial autocorrelation between microclimatic conditions and plants or other food sources will often constrain food availability and might result in tradeoffs between thermal, hydric and nutritional requirements.

Organisms not only interact within the environment, but also modify the state of the environment – the biotic interaction milieu [2]. In simple cases, feeding depletes resources or alters the behaviour of prey, whereas in other cases organisms act as ecosystem engineers and substantially fashion the local environment [68]. Processes such as trampling, consumption of the environment and pheromone deposition can act to alter the behaviour of individuals in characteristic ways. Thus, a ubiquitous form of environmental modification is trail formation. This acts as

a form of collective memory in which resource distribution and availability are encoded in the environmental structure through the process of reinforcement of frequently used trails and loss of those not used. Trail systems thus enable individuals acting locally to access accumulated and distributed information over much larger spatial and temporal scales [61,69].

Temporal dynamics and ecological coupling of nutritional traits

Nutritional responses are dynamic, changing in the short-term, over the course of development, trans-generationally via epigenetic parental effects and over evolutionary time scales [21,70]. Fundamental nutritional traits that might be subject to such changes have been quantified using GF models and include the intake target (IT), the growth target (GT), the relative value assigned by regulatory systems to maintain intake of different nutrients when on imbalanced diets [71], the extent to which excess ingested nutrients and toxins are voided rather than stored [70] and the strength of constitutive defences or induced responses having been attacked [72,73].

If traits influencing an organism's susceptibility to being consumed (e.g. the nutrient and PSM makeup of a plant) are under strong genetic control [72], then differential consumption can spread the effects of these genetic influences to other trophic levels. Hence, herbivory can act as a selective agent on apparently unrelated processes such as litter breakdown, soil mineralization and fine root production in terrestrial systems [74,75] and coral cover, macroalgal cover and bioerosion in marine systems [76].

Different heritabilities of traits and extents of spatial autocorrelation can establish heterogeneous foraging environments at multiple scales. For example, there is significant spatial autocorrelation in foliar concentrations of PSMs toxic to mammals over a distance of approximately 40 m in *Eucalyptus* forests [77]. Therefore, herbivorous mammals must move more than this distance to encounter significant variation in plant composition. The extent to which similar factors are important in the marine environment is unclear, although recent work suggests that algal secondary metabolite concentrations can be heritable [73].

Achieving synthesis: an integrating modelling framework

Having set out the component parts for an organism-based synthesis for nutritional ecology, what form might such a framework take?

An integrated modelling platform to link the nutritional biology of individual organisms to ecological processes across multiple scales would involve resource-seeking agents (organisms, both consumers and consumed) interacting locally and evolving within dynamic environments. The core aims would be:
1. To develop a generic model structure to represent individual agents, which can be parameterized to represent any specific type of organism and released to operate freely within the simulated environment;
2. To implement well-defined rules that describe how agents interact with each other and with their environment;
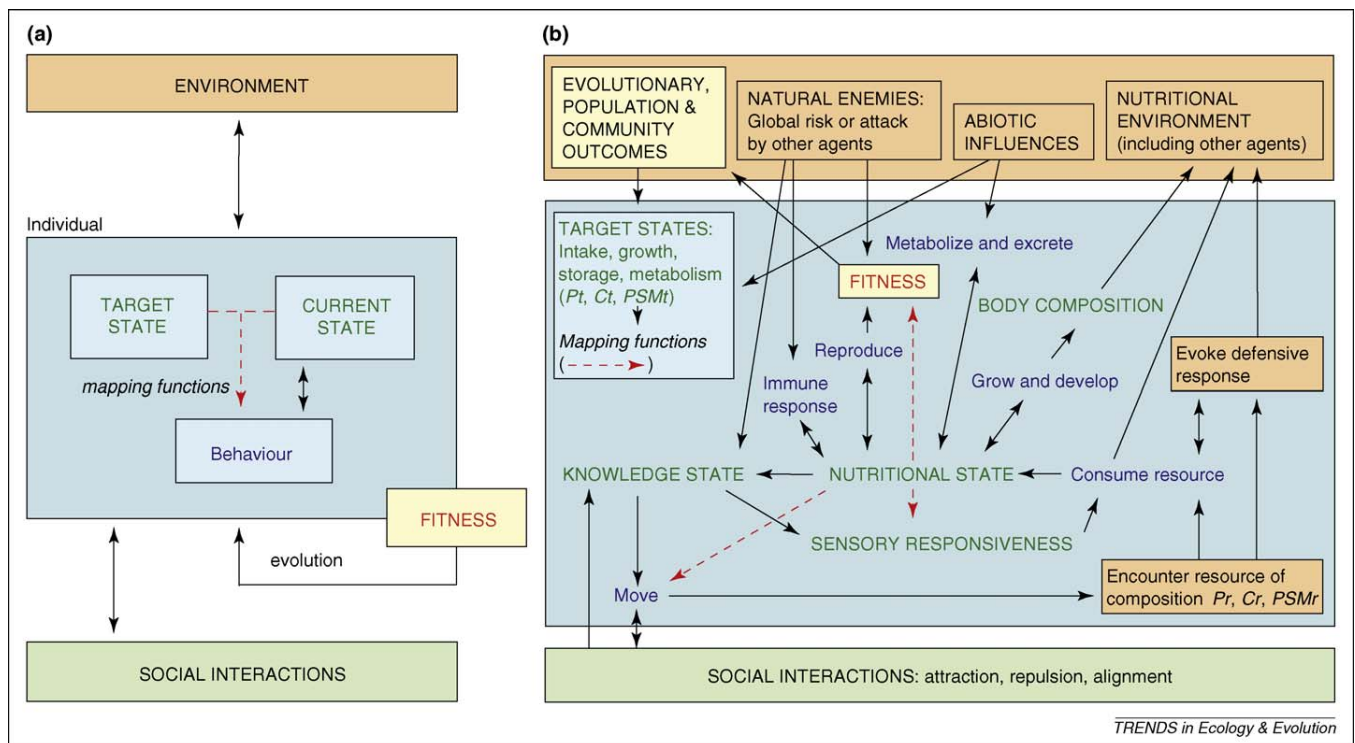
Figure 2. (a) Simplified and (b) expanded flowcharts representing a general model for a foraging agent. Solid arrows represent influences; dashed lines are mathematical mapping functions based on the difference between the current and target states of the agent. Terms in green upper-case letters are states and conditions and those in lower-case blue letters are behaviours. Buff-coloured items indicate environmental properties and the other items in the shaded blue rectangle are agent properties. Resource and target P, C and PSM are protein, non-protein energy (carbohydrate + fat) and plant secondary metabolites, respectively.
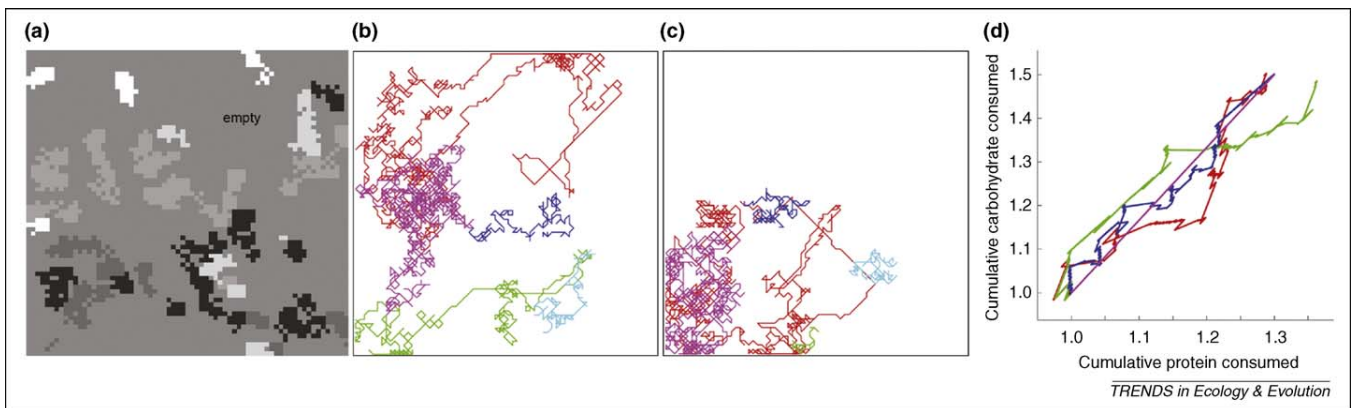
Figure 3. Agent-based nutritionally and spatially explicit simulation model. (a) Agents exist in a climatically uniform landscape containing patchily distributed food resources (which, for simplicity, are not reactive agents). The total number of food items in the environment is fixed and resource distribution is set according to a fractal algorithm. Food resources are of fixed total nutrient content but differ in protein to carbohydrate ratio. These ratios are represented as shades of grey from 1P:0C (white) to 0P:1C (black). Foods are non-renewable; once consumed they do not grow back. The agents have no memory and consider only current and adjacent locations when determining whether and how much to eat or whether to move. (b,c) Tracks for simulated agents as they move, optimising fitness by minimising the distance between their current and target nutritional states. In (b) the agents tend to avoid each other, whereas in (c) they tend to aggregate. (d) Trajectories of three agents in nutrient space, one from a population of aggregating agents (green), another from agents that avoid each other (red), and the third from a group that ignore each other (blue). The target line is shown in magenta. When 100 runs of 25 agents per run were simulated in the same initial environment, there were highly significant effects of social strategy (three were tested: ignore, avoid, attract). The Euclidean distance from the intake target integrated over each agent's lifetime (which provides a measure of the extent to which agents were successful in maintaining an optimal nutritional state) was lowest (i.e. regulation was most effective) in the groups of agents that aggregated and highest in those that ignored other agents [mean (SE) 0.089 (0.0007), 0.104 (0.0067) and 0.308 (0.0138) for attract, avoid and ignore, respectively; $F_{2, 297} = 190$; $P < 0.0001$]. This indicates that grouping improved the locating of nutritionally limiting resources. However, owing to resource depletion, this advantage of grouping was eventually counterbalanced by local food shortage and competition, leading to earlier death in agents that grouped ($F_{2, 297} = 511$; $P < 0.0001$). Addition of alignment responses and cannibalistic encounters would be expected to ameliorate these effects and lead to migration and enhanced probability of locating new resources [25].

3. To generate simulated environments that encapsulate key features at multiple spatial scales and that respond dynamically to the activities of agents operating within them; and
4. To allow agents to adapt and evolve in response to their environments, e.g. by implementing learning and genetic algorithms.

Individual agents would need to be characterized by as many pertinent traits as are needed for the questions to be addressed while avoiding excessive detail that would jeopardize simplicity, tractability and generality [4]. Ideally, the model should be sufficiently general so that, by adjusting specific parameter values, the same model structure could be used to represent a wide range of organisms and situations. By setting sensible default values, it should be possible to tailor the model for use at several interacting levels.

The basic elements of model agents are set out in Figure 2 and are as follows:

1. Behaviours, defined broadly as things the agent does, e.g. feed, move, defend (immediate defensive and longer-term induced responses, including immune responses), metabolize, grow, excrete, develop and reproduce.
2. States and conditions of the agent, which determine what the agent does. These determine, and in turn are affected by, the agent's behaviours, and include nutritional state and levels of toxins and other non-nutrients ingested with food, developmental stage, age, sex, size and knowledge state (sensory capabilities and other information the agent has about its environment).
3. The agent's position in space and time, both within its environment and in relation to other agents.

Agents would be set free to interact within simulated environments. Each agent would have a nutritional com-

position and some capacity to prevent access to those nutrients by other agents, which would determine whether, and to what extent, the agent is eaten. Having eaten, the consumer would change state and behaviour accordingly. Evolutionary change could be implemented in simulations by allowing target states, behaviours and linking functions to be mutable.

We show an example of a simple prototype simulation in Figure 3. In this case there is a single type of agent foraging within an environment in which foods containing different ratios of protein and carbohydrate but no toxins are distributed patchily. The agents have no memory but are able to track their intake target by matching the quality of a given food with the current nutritional state.

Conclusions

We have considered the requirements for an organism-based perspective to obtain a synthesis for nutritional ecology. In our view such models need to be nutritionally, organismally and ecologically explicit, as well as dynamic and spatially explicit across multiple temporal and spatial scales, if they are to serve as an interface for integration across the interacting levels of biological organization. Tools that offer promise for such integration include ABMs, state–space geometric models of nutrition and models representing environments across multiple spatial scales. We can envisage three major themes comprising a modelling programme for nutritional ecology, broadly defined as modelling of nutritional phenotypes, of populations and of communities. Some of the questions that might be addressed within each of these are listed in Box 1. To address such questions, increased focus is needed on investigations that span the boundaries separating sub-disciplines [78]. We believe that achieving this integration in a modelling platform will provide an important scaffold for greater synthesis across the ecological and functional sciences.

Box 1. Questions to be addressed using heterarchical models of nutritional ecology.

Three themes for modelling nutritional interactions from an agent-based perspective, with examples of questions that could be addressed in dialogue between modelling and experiments.

Modelling phenotypes
- What is an optimal memory length for consumers in spatially, temporally and chemically heterogeneous environments?
- What is the significance of nutritional heterogeneity and predation pressure on the evolution of diet breadth?
- Which search strategies evolve in different environments?
- What phenotypic traits do successful invasive species possess?
- How do nutrition and life histories change along environmental gradients (e.g. in temperature)?
- To what extent do microclimatic conditions constrain the times and places where organisms can obtain nutrients?

Modelling populations
- Does information transfer evolve within groups that forage in heterogeneous environments?
- Which environmental features encourage aggregation and mass movement by animals?
- Under what circumstances do populations of generalist consumers (i.e. individuals that are capable of utilising a wide range of foods) prosper compared with populations of local specialists?
- To what extent can metapopulation dynamics be explained by nutritionally motivated movements?
- How do performance–response landscapes for individuals translate into population growth responses?

Modelling communities
- How do nutrient balancing and toxin avoidance by herbivores interact to determine the spatial distribution of plants and the optimal allocation of defensive compounds between tissues within plants?
- How do patterns of succession arise within plant communities?
- What are the consequences of adding trophic levels (represented as classes of phenotype with differing, predefined trait values) to food web structure, trophic dynamics, direct and indirect interactions and intra-guild predation?
- Is it possible to evolve plants and animals beginning with a single population of primordial agents with phenotypic traits derived from a common distribution of genetic variants?
- How resilient are species assemblages and ecosystems to disturbance?

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