From metabolism to coexistence: Understanding animal movement and community dynamics through energy

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Abstract

Recent advances in the field of movement ecology have revealed intricate links between the movement of individual animals and the biodiversity of ecosystems. Hence, to advance our understanding of biodiversity and its ongoing loss due to global change, we may benefit from considering animal movement processes. Movement both shapes and is shaped by an animal's energy state. Additionally, fitness, and ultimately population dynamics, depend on energy allocation to survival, growth, and reproduction. Consequently, integrating energetics into frameworks that link movement and biodiversity is a logical next step to uncover how individual-level processes shape species dynamics within communities. Here, we propose a conceptual framework linking animal energetics, movement behavior, and community dynamics to explore how energy fluxes drive movement, mediate species interactions, and shape coexistence. The energy available to an animal motivates and constrains movement, while behaviors that maximize net energy gain, by minimizing costs and maximizing intake, affect fitness, species interactions, and community structure. This perspective reveals how energy dynamics can drive decisions on whether, how, where, and when animals move, and how energy-based equalizing mechanisms (e.g., similar energy balances among species) and energy-based stabilizing mechanisms (e.g., energy costs that limit large populations) underpin coexistence and biodiversity patterns. By synthesizing insights from community ecology, movement ecology, and ecophysiology, we advocate for a novel mechanistic approach to understanding diversity dynamics and predicting the impacts of environmental change on biodiversity. We call for the development of interdisciplinary methods to address key open questions in this area and provide examples of how this framework can be applied to advance understanding across varied ecological systems.

Keywords: Animal movement energetics, Energy dynamics, Equalizing and stabilizing mechanisms, Community theory, Biodiversity conservation, Individual-based ecology

Introduction

Understanding when and how species coexist is one of the great challenges in ecology (Chesson, 2000; Hubbell, 2001; Hutchinson, 1978, see Glossary in Box 1 for definitions). Following modern coexistence theory (Chesson, 2000), mechanisms that promote species coexistence can either be equalizing (reducing fitness differences between species), or stabilizing (increasing intraspecific competition over interspecific competition). Examples of such mechanisms in animals include resource partitioning (an equalizing mechanism, e.g. Hood et al., 2021) or prey switching by predators (a stabilizing mechanism, e.g. Vallina et al., 2014). These mechanisms are often mediated by animal movement, for which extensive data are now available (Jeltsch et al., 2013; Williams et al., 2020). However, movement data alone often fail to reveal why an animal begins moving, selects a particular direction, or what trade-offs are involved. This lack of understanding impedes accurately predicting species- and community-level processes (Costa-Pereira et al., 2022). By better understanding the movement decisions of individual animals and the factors that influence them, such as their physiological state, we can gain a more mechanistic understanding of the causes and consequences of movement behavior and the connections between movement and community-level processes like species coexistence.

There are several mechanisms by which the movement of individual animals influences the dynamics of species communities and in turn patterns of biodiversity. Mobile link effects arise from individuals transporting other individuals, propagules, or genes (e.g. Lundberg & Moberg, 2003), while direct interaction effects occur through all types of movement, e.g., dispersal, migration, and daily foraging (Jeltsch et al., 2013; Schlägel et al., 2020a). For instance, dispersal connects communities and drives spatial turn-over in metacommunities (e.g. Logue et al., 2011). The classical trade-off between dispersal ability and competitive performance, known as the colonization-competition trade-off, directly links movement and coexistence (e.g. Cadotte et al., 2006). Migration can induce competition among migrants or between migrants and residents (Holdo et al., 2011), and daily foraging movements mediate competition for resources that are spatio-temporally heterogeneous (e.g. Buchmann et al., 2012; Wilson et al., 1999). Generally, the distribution of individuals in space scales to the community level through encounter rates and aggregation of individuals, which influence competition, predator-prey dynamics, and other interactions (Schlägel et al., 2020a). Recent research has expanded on links between movement and biodiversity, revealing insights such as the role of individual personalities in mediating species coexistence (Milles et al., 2020; Rohwäder et al., 2024), the impact of variations in dispersal strategies on local community composition (Parry et al., 2024, see Glossary), the effect of species mobility in fragmented landscapes on community assembly (Szangolies et al., 2022; Teckentrup et al., 2019), and the role of individual movement decisions in driving disease transmission and community persistence (Scherer et al., 2020). These examples highlight a growing interest in integrating movement processes into research on coexistence and biodiversity.

However, movement itself is influenced by another factor: energetics. Energetics encompasses both the energy available in the landscape and an individual's energy demands and reserves (Halsey, 2016; Shepard et al., 2013). Optimal foraging theories have long been used to predict how animals move to maximize their energy intake (Charnov, 1976). However, these theories often overlook or are highly simplistic in their consideration of costs associated with movement (Klappstein et al., 2022). Alternatively, the concept of energy landscapes has been formulated to encompass not only the rewards from foraging in a given location but also the costs of moving there, both of which shape an individual's decisions. The costs of moving around are not trivial and depend on various factors, including the landscape (e.g., terrain), individual state (e.g., mass, reproductive state, or fat storage), movement mode (e.g., flying, swimming) and characteristics (e.g., speed), movement strategy (Klarevas-Irby et al., 2021), and the presence of other individuals moving similarly (i.e., collective motion; Zhang & Lauder, 2023). While animals may move for various reasons such as to avoid predation, socialize, or breed, energy represents a fundamental currency of life necessary for survival and reproduction (Burger et al., 2021). Thus, the balance between energy gains and expenditure plays a crucial role in determining whether, how, where, and when an animal decides to move. Measuring this balance or simply the total costs of movement in the field remains a challenge, but ongoing advances in accelerometers and other sensors may allow for more insights in the future (Fuller et al., 2020; Williams et al., 2021; R. P. Wilson et al., 2020). In addition to such field methods, simulation models have emerged as valuable tools for exploring the drivers and consequences of movement decisions. These models allow researchers to simulate energy costs across diverse scenarios, illuminating how movement and other energy expenditures influence higher-level ecological processes, such as individual survival, species interactions, and community dynamics (Chimienti et al., 2020a; Gallagher et al., 2021b; Malishev & Kramer-Schadt, 2021a; Szangolies et al., 2024, see Glossary).

Given the established links between movement and community dynamics, as well as between movement and energy dynamics (see Glossary), a natural next step is to explore the connection between energetics and species coexistence. Here we aim to establish a triangle of interactions among animal energetics, movement behavior, and coexistence (Figure 1). We then present a detailed conceptual framework illustrating the processes that link energetics, movement behavior and community dynamics. We begin by elaborating on key concepts of animal energetics, setting the stage to highlight mechanisms linking energetics with movement and energetics with coexistence. With this foundation, we propose future research directions to further advance ecological theory and enhance biodiversity conservation.

Energy balance: The relationship between energy intake and energy expenditure (Caballero, 2005). A positive energy balance occurs when energy intake exceeds energy needs and a negative energy balance indicates an energy deficit.

Energy expenditure: The total amount of energy used by an individual over a given period, such as a day (Caballero, 2005).

Energy budget: The total amount of energy acquired by an individual and then allocated across various biological processes, including maintenance and survival, growth, reproduction, and movement (Kooijman, 1986).

Energy dynamics: The processes of energy intake, allocation, and expenditure, and how these change over time.

Coexistence: The pattern in which different species occur in the same place while maintaining stable populations over time (Blanchet et al., 2020; Chesson, 2000).

Co-occurrence: The presence of multiple species at the same location, which may occur randomly, but can lead to coexistence under certain conditions (Blanchet et al., 2020).

Coexistence mechanisms: Processes that enable competing species to coexist. Modern coexistence theory proposes two mechanisms: Equalizing mechanisms, which reduce fitness differences, and stabilizing mechanisms, which increase intraspecific competition relative to interspecific competition (Chesson et al. 2000).

Community assembly: The processes that determine the identity and relative abundance of species which coexist in an environment (Kraft & Ackerly, 2014).

Community composition or community structure: The relative frequencies and identities of co-occurring species.

Community dynamics: Changes in community composition or structure over time.

Movement ecology paradigm: Conceptual framework in movement ecology which focuses on how internal state, motion capacity, and navigation capacity of individuals are influenced by external factors to produce emergent movement paths (Nathan et al. 2008).

Box 1: Glossary

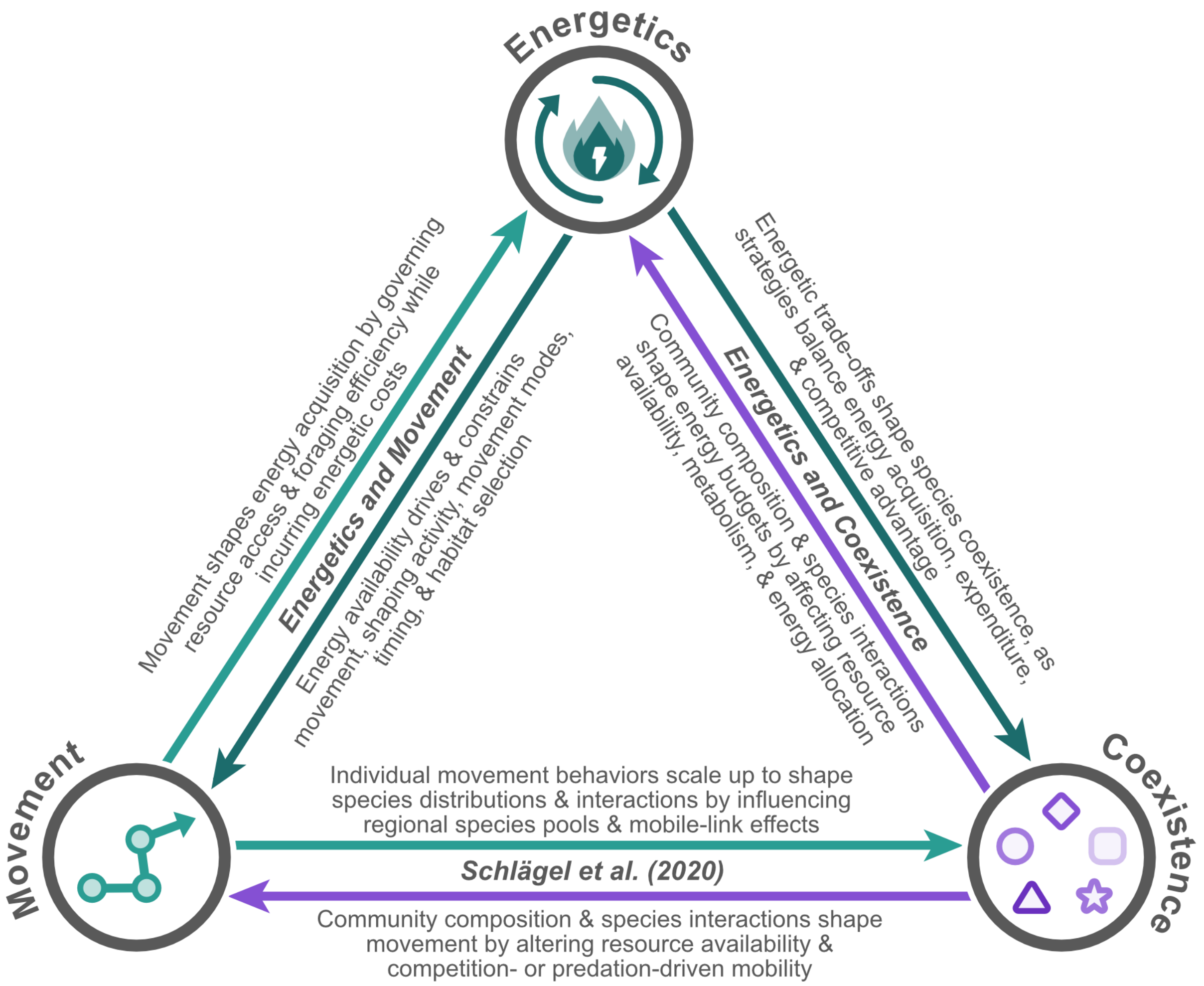

Figure 1: Triangle of interactions among animal energetics, movement, and coexistence. Links between energetics and movement, and energetics and coexistence are detailed in the manuscript (section names in bold italics), while movement–coexistence links are described in Schlägel et al. (2020). Brief descriptions of the links are given along the directive arrows which indicate interactions.

Key concepts of animal energetics relevant for movement and community dynamics

Energy, obtained through food consumption, fuels all life processes, including survival, growth, reproduction, and movement (Brown et al., 2004). Understanding how animals acquire, manage, and use energy is therefore central to interpreting how movement behaviors are shaped by ecological pressures and how these energetic processes influence community dynamics.

As animals move through their habitats, they acquire energy from foraging, which is ingested, digested, and then allocated or stored. Simultaneously, they expend energy to meet their total energy expenditure, encompassing the costs of all life processes—collectively termed field metabolic rate (Nagy, 1987). The net energy change at any given moment may be positive, neutral, or negative, determining whether reserves are built, maintained, or depleted. This relationship between energy intake and expenditure is referred to as an animal’s energy balance (see Glossary). During periods of negative energy balance, when energy intake falls short, animals must draw from their reserves, potentially compromising fitness-related processes (Sibly et al., 2013).

To prevent depleting reserves too much, trade-offs occur between maintenance, movement, growth, and reproduction, as energy used for one process becomes unavailable for others. Movement, in particular, is a highly dynamic and energetically expensive process, with costs influenced by intensity, duration, and environmental conditions (Halsey, 2016; Shepard et al., 2013). Growth and reproduction also demand substantial energy investment: growing animals require energy for tissue development, while reproduction involves additional costs for tissue synthesis, gestation, egg and sperm production, lactation, and parental behaviors (Ginther et al., 2024; West et al., 2001).

During periods of energy limitation or when approaching ‘metabolic ceilings’ (e.g., Speakman & Król, 2010), animals employ diverse strategies to navigate these trade-offs, which vary with life history traits, behavioral types, and diets. Some species may increase movement to locate richer resources, while others can conserve energy by reducing activity or entering states like torpor. These strategies affect fitness and recruitment, influence species interactions, resource use, and niche partitioning, and can have cascading effects on population and community dynamics. As an example, in several detailed studies on European badgers (*Meles meles*) using long-term datasets, accelerometers, and doubly labeled water, Bright Ross et al., (2021, 2024) found substantial inter-individual variability in energy expenditure among badgers in the same environment, with age, body condition, and weather influencing survival and reproductive success. Young and reproductive badgers invested more in activity, correlating with lower body condition in the following season. However, these groups with higher activity costs were also found to have a lower mortality risk at a given body condition, suggesting they could increase activity when needed without a corresponding rise in mortality risk. In contrast, older individuals minimized energy expenditure and were less active, conserving energy to enhance survival. These diverse energy-budgeting strategies, shaped by age, reproductive stage, and individual behavior, might contribute to the population's resilience to environmental changes.

Several conceptual models explain how animals manage energy across competing demands, particularly in relation to movement (Careau et al., 2008, 2021; Mathot & Dingemanse, 2015). The additive model posits that activity expenditure adds linearly to maintenance costs, while the performance model suggests higher activity necessitates greater metabolic capacity, increasing both maintenance costs and field metabolic rate (Careau et al., 2021). In contrast, the constrained model proposes a fixed energy budget (see Glossary), with increases in activity offset by compensatory reductions in other processes, such as reproduction or immune function (Careau et al., 2021). Bioenergetic simulation models interpret these trade-offs differently: some allocate energy in fixed proportions (Kooijman, 2000; Martin et al., 2012), some follow a sequential prioritization of metabolic processes (Sibly et al., 2013), and others use optimization strategies to guide allocation based on individual state, e.g., body condition or life stage (Kozłowski, 1992; McNamara & Houston, 1996). However, aside from a few examples, most models do not explicitly consider the costs of activity or trade-offs between movement and other processes, instead treating activity costs as a fixed component of maintenance (see Malishev & Kramer-Schadt, 2021 for a review of movement-explicit simulation models).

Understanding how movement integrates into energy budgets is essential for predicting how animals respond to ecological pressures, such as resource scarcity, predation risk, or environmental change, and for linking individual behaviors to broader patterns of coexistence and community structure.

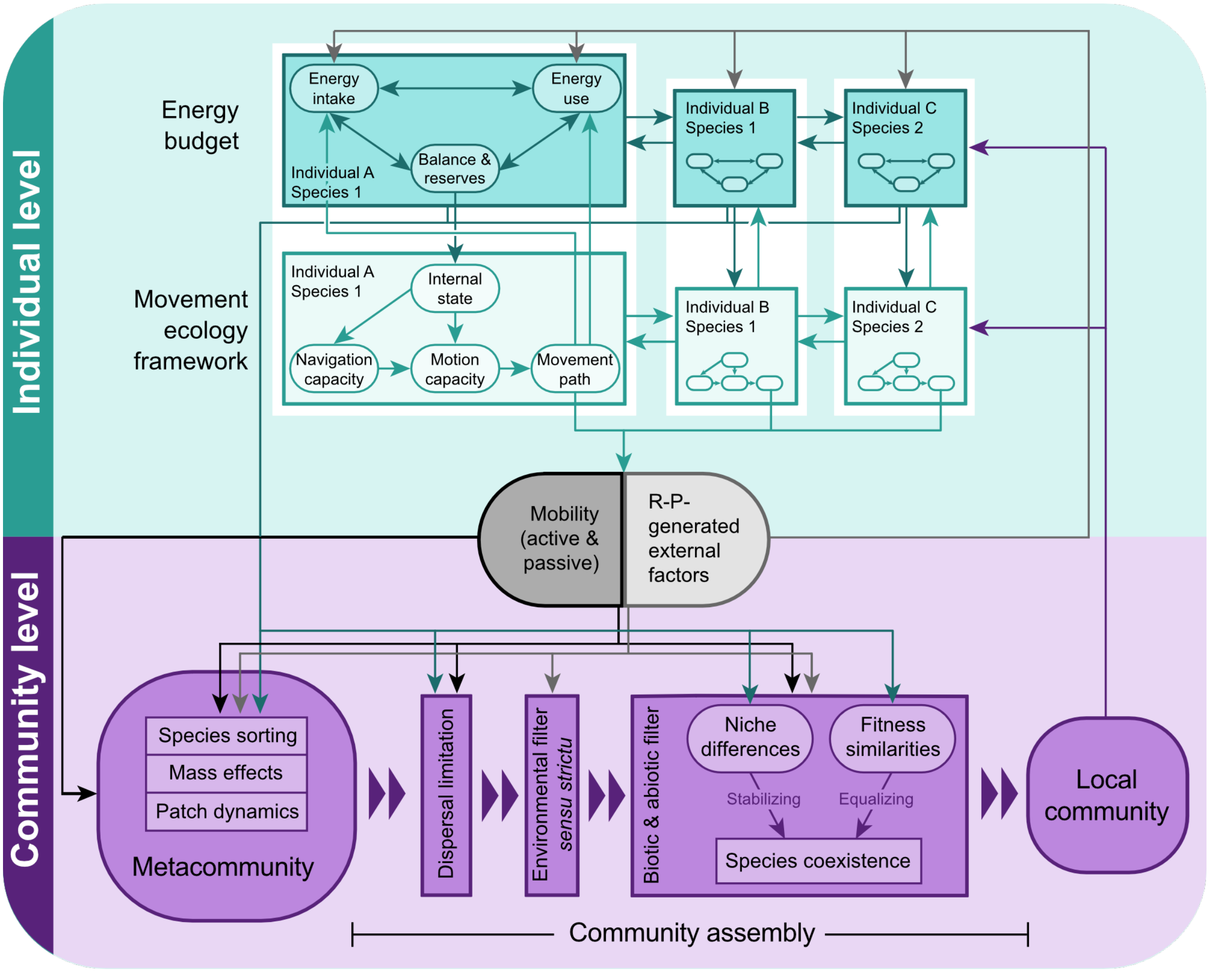

Figure 2: Conceptual framework linking energy budget theory with the movement ecology framework on the individual level, and integrating concepts from metacommunity theory, community assembly and coexistence theory on the community level. Movement (in light teal) and energetics (in dark teal) scale up to the community level (in purple) through resource and process links affecting the environment (R-P-generated external factors), as well as through direct links between energy budgets, metacommunity processes, and coexistence mechanisms. Square boxes depict processes, rounded shapes represent patterns, and arrows indicate links of processes and patterns. This framework is adapted and extended from Schlägel et al. (2020) to consider energetics.

An integrated framework for linking animal energetics, movement, and coexistence

Schlägel et al. (2020) proposed a framework uniting the established movement ecology paradigm (Nathan et al., 2008; see Glossary), and resulting interactions among individuals, with key concepts from metacommunity theory, community assembly, and coexistence theory. We here limit our discussion of the link between movement and coexistence, as it has been thoroughly addressed in prior research. Instead, we extend the framework presented in Schlägel et al. (2020) in detail by incorporating individual energy dynamics, exploring their connections to movement, environmental conditions, and community dynamics (Figure 2). Energy budgets are a natural fit within this framework due to their close relationship with movement and coexistence mechanisms (see Glossary).

Movement is driven in part by an animal's internal state, or the physiological and neurological status of the focal individual that affects its motivation and readiness to move (Nathan et al., 2008). Energetic drivers and costs of movement decisions and behaviors may directly influence this internal state, deciding whether and how an animal actually moves (Figure 2, top panel). These decisions may be driven by energy balance and reserves, which result from energy intake and energy expenditure (details in the Energetics and Movement section below). However, the realized movement, which results from an individual's internal state (‘why (or why not) to move?’), motion capacity (‘how to move?’), and navigation capacity (‘when and where to move?’, Nathan et al., 2008), incurs costs which influence animal energy expenditure and feed back into the energy budget process.

The movement of individuals scales up to species-level mobility driving interactions within and between species and influencing abiotic and biotic environmental conditions, such as through resource competition, that underpin metacommunity- and community-level processes (Figure 2, lower panel). The formation of local communities can be conceptualized as a series of filters through which species from a regional species pool must pass, more described in the following. The regional species pool, or metacommunity, is shaped by habitat heterogeneity and environmental filtering (species sorting), spatial dynamics via dispersal (mass effects), and trade-offs between local competitive and dispersal abilities (patch dynamics). The processes filtering this metacommunity into a local community are known as 'community assembly' (HilleRisLambers et al., 2012; Kraft et al., 2015). Filters are influenced by the environment (Resource-Process (or R-P) generated external factors), species mobility, and species-specific energetic traits. For example, species must be able to reach a habitable location, which depends on their energetic reserves and mobility (dispersal limitation). Additionally, the environment must provide suitable abiotic conditions for the species, including favorable temperature regimes (environmental filtering). Finally, the species must successfully interact with other species, and these biotic interactions often interplay with abiotic factors (biotic and abiotic filtering). For example, where temperatures favor the productivity of species such as ants, competition plays an important role in the structuring of communities (Boet et al., 2020). In contrast, environmental filtering *sensu stricto* specifically examines the effects of abiotic conditions on species survival in the absence of other species (Kraft et al., 2015).

With respect to the biotic filter, coexistence theory proposes two mechanisms that promote species coexistence. Links between species mobility and these coexistence mechanisms are well established (Jeltsch et al., 2013; Milles et al., 2020; Schlägel et al., 2020a). We will detail below, how individual energy dynamics can influence these coexistence mechanisms (Energetics and Coexistence section).

Together, these filters determine which species form the local community. This community, in turn, shapes the movement and energy dynamics of its members through interactions such as competition, resource partitioning, and predation, creating feedbacks that influence coexistence and community structure.

To illustrate the interactions, trade-offs, and feedbacks within this framework, consider an individual animal foraging to meet its energy demands. If the animal is unable to find sufficient food locally, its energy balance and reserves begin to decline, prompting it to seek food in other areas. However, this movement incurs energetic costs, and the animal must weigh the potential benefits of energy gain against the costs of movement. As its energy stores dwindle and intake remains insufficient, the need to find more profitable areas becomes critical for survival. The animal’s current energy state and mobility limit its ability to reach distant locations (dispersal limitation). Even when it does reach new areas, only some may provide suitable conditions for survival (environmental filtering).

Upon arrival, the presence of other individuals, possibly from different species, introduces the potential for competition for resources. If these individuals consume different resources (niche differentiation), or if they can achieve similar energetic outcomes and maintain comparable fitness levels (fitness similarity), coexistence becomes possible, allowing the individual to integrate into the local community. Ultimately, the individual's death will release the energy stored in its body back into the environment, becoming available to other species through predation, scavenging, or decomposition.

In the following sections, we explore the connections between individual energetics, movement ecology, and community dynamics in greater detail, supported by theoretical foundations and empirical examples.

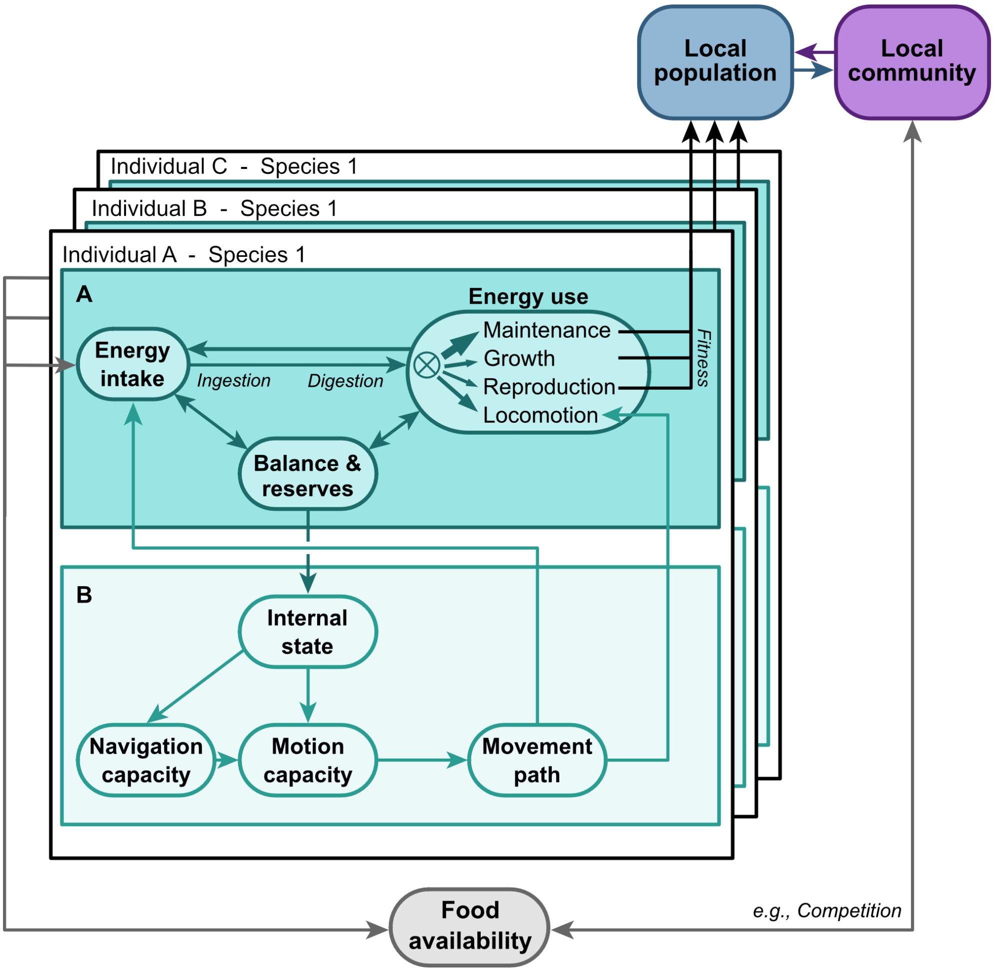

Figure 3: The links between individual energy budgets (A) and movement (B). Foraging movements allow for energy intake but also incur locomotion costs (light teal arrows). Ingested energy is allocated to various metabolic processes, including digestion, maintenance, locomotion, growth, and reproduction. The distribution of energy among these processes impacts individual survival, growth, and reproductive output, which, in turn, influences population dynamics (in dark blue) and, ultimately, the local community (in purple). Arrow size in the 'Energy use' box provides an illustrative snapshot of how available energy could be allocated among processes. When energy balance is positive, meaning energy intake exceeds costs, surplus energy can be stored as body reserves for future needs. Changes in energy dynamics drive the internal state to motivate movement (light teal). Changes in food availability and the densities of conspecifics and heterospecifics drive competition, limit energy intake, and shape local community dynamics. This figure highlights key energy pathways linking energy dynamics, movement, and coexistence, though it may not be exhaustive.

Energetics and Movement

The relationship between energetics and movement is fundamental, as energy derived from metabolic processes fuels locomotion (Figure 2 top panel, Figure 3A). At the cellular level, muscle contractions, essential for all movement, depend on this energy. Although the cost of locomotion can substantially elevate daily energy expenditure (Halsey, 2016), mobility provides the advantage of accessing resources that remain out of reach for sedentary species.

Scientific interest in the links between locomotion and energy use dates back over 125 years, with early studies examining the energetic costs of movement (Zuntz, 1897). The field saw rapid advancement during the 1970s and early 1980s (Garland, 1983; Schmidt-Nielsen, 1972; Taylor et al., 1970) largely driven by the development of respirometer devices, which allowed for more precise measurement of energy expenditure associated with locomotion. Today, the field is experiencing a resurgence thanks to bio-logging devices that can record proxies of activity and energy expenditure, including acceleration and heart rate, in wild animals (Fahlman et al., 2021; Wilmers et al., 2015). However, much focus so far has been one-sided, emphasizing the measurement of locomotion energy costs, and their relation to intrinsic factors such as body mass, morphology, or speed. In contrast, the role of physiological mechanisms in driving movement behavior and the complex interplay between energetics, movement behavior, and other aspects of physiology have received less attention. However, recent studies have begun to explore the connections between physiology, short-term activity, exploratory behavior, and dispersal, revealing the intricate interplay between an animal's internal state and its movement strategies (Wu & Seebacher, 2022).

Conceptualizing these links between physiological state and movement, Figure 3 showcases how movement both shapes and is shaped by an animal's energy balance. An individual of a particular species takes in energy from its environment and uses it to fuel various metabolic processes, which together determine its energy balance and reserves (Figure 3A). These energy dynamics influence the animal's internal state, shaping its decisions about whether, how, when, and where to move (Figure 3B). These movement decisions, in turn, determine the animal's path and affect both its energy intake—based on the food available at its chosen location—and the energy it expends on locomotion. The energy spent on movement can trade off with other energetic demands, such as maintenance, growth, and reproduction. Together, these processes drive the animal's fitness, influence population dynamics, and shape the structure of the local community.

Here, we synthesize current knowledge from both perspectives—how energy dynamics influence movement and how movement impacts energy dynamics—highlighting the drivers and consequences of animal decision-making regarding the fundamental questions of: why move, how to move, and when and where to move (Nathan et al., 2008).

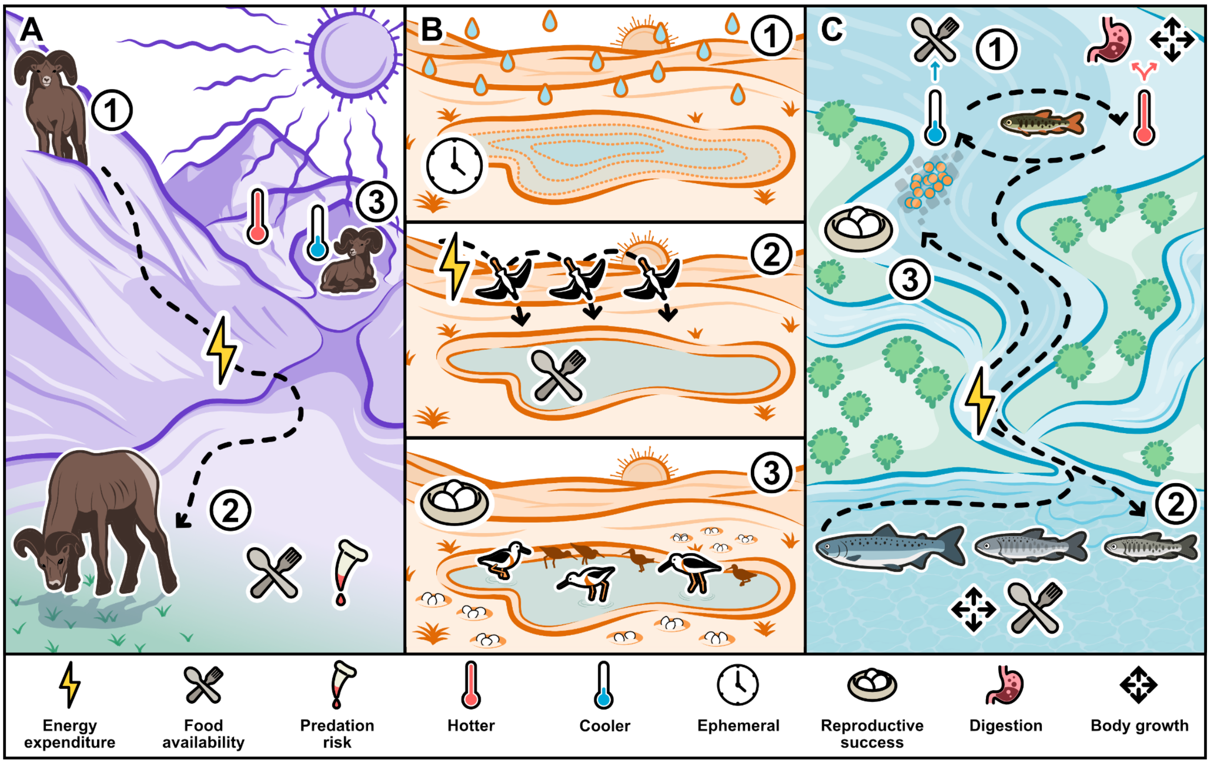

Figure 4: Examples of how energetics can be linked to decisions about whether to move (A), how to move (B), and when and where to move (C). The decision of whether to move can depend on body condition, as seen in Sierra Nevada bighorn sheep (Ovis canadensis sierrae), where individuals with higher energy reserves remain at high elevations and conserve energy (A1), while those with lower reserves migrate to access better food resources, despite increased predation risk (A2) (Denryter et al., 2024). Resting behavior may also provide energetic benefits, such as in hot conditions, where desert bighorn sheep (Ovis canadensis mexicana) can minimize thermoregulatory energy and water costs by resting in caves during midday to avoid heat stress (A3) (Cain et al., 2008). Movement strategies (how to move) can also be shaped by energy intake prospects, as in banded stilts (Cladorhynchus leucocephalus). They track ephemeral water bodies across Australia (B1), using long and potentially energetically expensive nomadic movements (B2) to locate food-rich areas which are essential for reproduction (B3) (Pedler et al., 2014). Timing and location of movement (when and where to move) can vary on different scales even within a species, as in coho salmon (Oncorhynchus kisutch). During resource pulses, juveniles undergo daily migrations, feeding in cold, food-rich habitats and moving to warmer areas to optimize digestion and growth (C1) (Armstrong et al., 2013). After a year or more, when conditions such as body size, abiotic factors, and food availability are favorable, they migrate to the sea to exploit higher resource availability and achieve faster growth (C2). Upon growing sufficiently to reach maturity, around 18 months later, they return to their natal streams to spawn, lay thousands of eggs, and ultimately die (C3) (Sandercock, 1991). Their eggs and carcasses then contribute to seasonal resource pulses, feeding other Pacific salmon and various consumers (Armstrong et al., 2013). Meanings of icons in the panels are explained in the legend below.

The energetic basis of why (or why not) to move

Energy serves as both a motivator for and a cost of movement. Foraging movements provide the benefit of energy acquisition, but also incur costs associated with locating, obtaining, and digesting resources (Figure 3). Animals must forage sufficiently to cover fitness-related costs, yet the search for resources always carries uncertainty of success. In the short term, hunger dynamics play a significant role in foraging behavior, with animals potentially driven by the state of their energy stores ('internal state' in Figure 3). For example, dual-intervention point theory posits that animal body fat is regulated to balance the risk of predation and the ability to survive periods of illness or food scarcity (Speakman, 2014). In Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), individuals with lower body fat reserves were found to be more likely to migrate and traverse greater elevational distances to reach areas with higher food availability, reducing starvation risk (Figure 4A). However, this strategy came with the trade-off of increased predation exposure (Denryter et al., 2024). When faced with stressors such as hunger and food shortages, vertebrates undergo a physiological cascade that triggers the production of stress hormones, which can drive observed changes in movement behavior (Creel et al., 2013; Goossens et al., 2020).

In the long term, individuals need to move to acquire energy not only for immediate survival but also to invest in processes such as reproduction and growth (Figure 3). In some situations, however, it may be more advantageous to rest and conserve energy rather than expend it searching for food (Denryter et al., 2021). Strategies such as torpor, hibernation, or aestivation enable animals to endure unfavorable conditions by reducing energy demands (Staples, 2016). For instance, house mice (*Mus musculus domesticus*) exhibit increased rates of torpor in response to higher foraging demands, represented by the travel distance required to secure a food reward, suggesting a plastic response to energy scarcity (Schubert et al., 2009). Similarly, in the marsupial Monito del monte (*Dromiciops gliroides*), chronic calorie restriction triggers increased torpor frequency and reduced daily energy expenditure (Nespolo et al., 2022). Conversely, increased movement is often necessary to prepare for future energy demands, such as in prehibernation hyperphagia (Penteriani et al., 2022). Golden-mantled ground squirrels (*Callospermophilus lateralis*) provide a striking example, doubling their body mass and tripling their fat stores in the weeks prior to hibernation (Kenagy & Barnes, 1988). Thermoregulation may also play a role in movement decisions. Increased movement can offset thermal costs when animals are in a hypothermic state (Humphries & Careau, 2011), while the need to dissipate heat can limit locomotion to avoid hyperthermia (Dyer et al., 2023; Speakman & Król, 2010; Trondrud et al., 2023) (Figure 4A). Responses to heat stress, however, may strongly vary between species. For example, in a study of three coexisting African antelope species—springbok (*Antidorcas marsupialis*), greater kudu (*Tragelaphus strepsiceros*), and common eland (*Tragelaphus oryx*)—behavioral adaptations to heat stress depended on a variety of factors including habitat, mobility, and body size (Berry et al., 2023).

Hence, the internal state of an animal, driven at least in part by its energetic and physiological state, can motivate whether it decides to move (Figure 3). Factors such as fatigue and recovery from intense exercise (Birnie-Gauvin et al., 2023; Kramer & Mclaughlin, 2001), digestion either reducing (van Hoven & Boomker, 1985) or increasing (Gleiss et al., 2019) activity, pregnancy effects on locomotor performance (Dayananda et al., 2017; Noren et al., 2012), and infection or disease status on lethargy and performance (Binning et al., 2017; Grabow et al., 2024) are also closely tied to energy intake and allocation. Together with social, life history, and predation avoidance behaviors, these factors shape movement decisions.

Energetic strategies for how to move

The energetic costs and benefits of movement vary depending on how animals navigate their environments (‘motion capacity’ in Figure 3). Passive movement modes, like gliding or drifting on currents, conserve energy but limit navigational control, potentially reducing access to consistent energy sources. In contrast, active locomotion strategies, like running or swimming, offer greater control over navigation and the ability to seek out resource-rich areas, but they come with higher energy costs. The various locomotion styles additionally incur energetic trade-offs: walking and running offer stability and minimal resistance to external forces like drag, resulting in lower energy costs per unit time. In contrast, flying and particularly swimming are more energy-efficient per unit distance, making them ideal for long-distance movements like migration (Schmidt-Nielsen, 1972). However, for flying and swimming, even small increases in movement speed can lead to markedly higher energy costs, while costs of running tend to increase linearly with movement speed (Hedenström & Alerstam, 1997; Heglund et al., 1982; Hind & Gurney, 1997). For species capable of utilizing multiple movement modes, trade-offs can arise. In the Southern Beaufort Sea subpopulation of polar bears (*Ursus maritimus*), divergent movement strategies have emerged in response to reduced sea ice (Pagano et al., 2020). While the majority of the subpopulation remains on the ice during summer, a smaller portion has been moving to land. Bears which moved to land spent more time swimming and expended more energy than those staying on the ice. However, this strategy allowed them to access higher-quality foraging areas, potentially improving energy intake and offsetting increased locomotory costs (Pagano et al., 2020).

Travel speeds may be physiologically constrained, with maximum sustained speeds generally increasing with body mass. However, the largest animals may have lower top speeds due to reduced heat dissipation capacity, which imposes metabolic constraints (Dyer et al., 2023). Though animals can save energy during locomotion via several mechanisms including their posture, using pendulum-like limb movements, and by moving at speeds which allow them to use stored elastic strain energy or to optimize movement and reduce drag (Hind & Gurney, 1997; Reilly et al., 2007). Ultimately, the energy required for moving in a particular mode or at a specific speed influences how efficiently animals can travel and imposes limits on their capacity to sustain high speeds or long-duration movement. Consequently, the energy costs to move influence an animal‘s overall locomotor strategy. Moreover, while it has been theorized that moving alone versus in a group may lead to differences in locomotive costs, such as in flocking birds or schooling fish (Kelly et al., 2023; Weimerskirch et al., 2001), direct metabolic evidence for either energy savings or additional costs associated with collective motion is still largely lacking (Zhang & Lauder, 2023).

Different types of animal movement reflect diverse strategies for balancing energy acquisition, conservation, and expenditure. Station-keeping and home ranging movements may allow animals to remain near stable resources to maintain energy needs, but even routine movements to obtain resources can incur substantial costs (Boratyński, 2020). Additionally, home ranges may need to be defended from con- and heterospecifics to remain profitable, another energetically expensive endeavor (Ord, 2021). Dispersal, on the other hand, may in part be motivated by the need to locate new resources or habitats, especially when current conditions become less favorable (Matthysen & Clobert, 2012; Ronce, 2007). While dispersal can lead animals to locations with higher energy availability and reduced competition, it typically involves higher energy costs for exploration and travel (Benoit et al., 2020). However, animals can mitigate these costs by adjusting movement strategies during the transience phase. For instance, transient vulturine guineafowl (*Acryllium vulturinum*) travel farther distances but move faster and in straighter paths, thereby reducing the energetic demands of large displacements (Klarevas-Irby et al., 2021). This strategy allowed dispersing birds to travel 33.8% farther daily with only a 4.1% increase in energy expenditure, and without additional movement time. Nevertheless, dispersal can also reduce foraging opportunities and interim energy intake until a suitable habitat is found (Zollner & Lima, 2005). This requires that animals have sufficient energy stores before embarking on such journeys, while, in some situations, increased competition for resources may deplete body stores, triggering dispersal even when animals are in a compromised state (Baines et al., 2020; Bonte & De La Peña, 2009; Goossens et al., 2020). In contrast, migration is driven in part by knowledge of or responses to seasonal variations in energy availability (Milner-Gulland et al., 2011). This remarkable energetic feat allows animals to access remote areas with higher energy resources or more favorable conditions. However, migration involves substantial energy costs for long-distance travel, requiring some animals to be hyperphagic in the premigration season in order to accumulate adequate energy reserves for the journey (Odum, 1960). When resources are unpredictable and limited, nomadic movements enable animals to locate ephemeral or patchily distributed resources while avoiding resource depletion (Stratmann et al., 2021; Teitelbaum & Mueller, 2019). For instance, in the stochastic Australian desert, the banded stilt (*Cladorhynchus leucocephalus*) undertakes remarkably long and rapid continent-wide movements to track ephemeral wetland resource pulses that are critical for breeding (Pedler et al., 2014) (Figure 4B). Such movements highlight the challenges faced by fully nomadic species, which must remain in near-constant motion in the absence of reliable resources (Teitelbaum & Mueller, 2019), potentially making nomadism both energetically costly and risky.

Energetic drivers of when and where to move

Decisions regarding when and where an animal moves are shaped by its energetic state and the current or anticipated availability of local resources (‘navigation capacity’ in Figure 3). These movement decisions occur across various temporal scales, ranging from rapid adjustments made over seconds or minutes to daily behaviors and broader seasonal strategies. Diel movement patterns, for example, may be driven by energy management needs, such as the vertical migration of dogfish (*Scyliorhinus canicula*) from cold, deep resting waters to warmer, shallower foraging areas (Sims et al., 2006), or the horizontal migration of juvenile coho salmon (*Oncorhynchus kisutch*), which feed in cold, food-rich habitats and then move to warmer areas to boost digestive efficiency and growth (Armstrong et al., 2013) (Figure 4C). Extreme events like heat waves, with their associated risk of hyperthermia, can restrict daily movements and foraging activities (Semenzato et al., 2021).

Triggers of seasonal movements, such as migration, are complex and may vary widely among species, driven by both extrinsic factors (e.g., photoperiod, temperature) and intrinsic mechanisms (e.g., fuel stores, corticosterone levels, circannual rhythms) (Eikenaar et al., 2018; Fudickar et al., 2021) (Figure 4C). Migration often aligns with local resource dynamics, allowing animals to increase energy intake by tracking phenological shifts in resource availability across space (Abrahms et al., 2021). A notable example is "green wave surfing," where animals follow the seasonal progression of greening vegetation in an attempt to maintain high energy intake throughout the year (Bischof et al., 2012; Hering et al., 2022). These effects on ingested energy can influence energy reserves, as in the Greater Yellowstone Ecosystem, where female elk (*Cervus elaphus*) that synchronized their movements more closely with peak green-up during the growing season were observed to have greater fat reserves by September (Middleton et al., 2018). Additionally, other environmental factors including weather conditions, such as wind speed for birds (Bradarić et al., 2020) or temperature in ungulates (Denryter et al., 2021; Sheppard et al., 2021), can influence locomotion costs and the timing of movements.

Hence, the paths that animals follow and how they distribute themselves in space are driven by, and incur, energy costs (Klappstein et al., 2022). To maintain sufficient foraging efficiency, animals must balance energy gained against the costs of moving through environments which vary dramatically in terrain, microclimates, substrates, and vegetation, collectively shaping the energy landscape experienced by a species (Shepard et al., 2013; Wilson et al., 2012). While immediate environmental cues play a substantial role in guiding movement decisions and determining energy costs, animals may also rely on spatial memory of resource-rich locations (Abrahms et al., 2019; Nabe-Nielsen et al., 2013). However, under altered conditions, such as those expected with climate change, relying solely on memory could lead to animals returning to habitats that are no longer energetically viable. For instance, evidence suggests that blue whales (*Balaenoptera musculus*) depend on long-term memory of spring resource blooms, rather than tracking current ‘green-up’, which could lead to mismatches if environmental conditions change rapidly (Abrahms et al., 2019). In reality, animals likely use a combination of proximate cues, intrinsic factors, and spatial memory to decide when and where to move in order to meet their energy needs while managing energy costs (Merkle et al., 2019).

Energetics and Coexistence

Given the close link between individual energy dynamics and movement, as well as the relationship between movement and animal coexistence (Jeltsch et al., 2013; Schlägel et al., 2020), it is clear that energy dynamics influence species coexistence. First, energetics and physiology determine species' home range sizes, geographic distributions and extents, and performance (Boratyński, 2020, 2021; Claunch et al., 2023) and thus influence the possibility of co-occurrence and coexistence (see Glossary). Second, energy available for maintenance and reproduction directly impacts individual fitness, which plays a critical role in defining competitive advantages in species interactions (Hall et al., 1992; Lotka, 1922). Third, an organism’s internal energy status shapes its behavior and movement patterns, with these individual behaviors scaling up to affect broader community dynamics (Goossens et al., 2020). As Lotka (1922) suggested, “where the supply of available energy is limited, the advantage will go to that organism which is most efficient, most economical, in applying to preservative uses such energy as it captures”, highlighting the connection between energetics, behavior, and species interactions.

Although there are additional pathways through which energetics mediate coexistence, most studies have historically focused on the relationship between energetics and movement, with relatively limited research on how energy dynamics directly affect species coexistence. Brown et al., (1993) and Hall et al., (1992) were among the first to integrate energetics into the understanding of species distributions, but studies explicitly examining the relationship between energy dynamics at the individual-level and species coexistence have only recently emerged (Brandl et al., 2023; Szangolies et al., 2024). These concepts are yet to become well understood and widely applied. Species coexistence itself has been a focus of ecological research for several decades and has evolved substantially over time (Chesson, 2000; Hubbell, 2001; Hutchinson, 1978). Integrating energetics into this research discipline may further enhance theory and application.

Modern coexistence theory suggests two key mechanisms that govern species coexistence, both of which can be contextualized through the lens of animal energetics (Figure 2, lower panel, Figure 5). First, increasing niche differentiation has a stabilizing effect (Chesson, 2000). Niches, which describe the specific abiotic and biotic conditions under which species exist, are strongly shaped by the energetic and physiological needs of organisms (Tschapka, 2004). From this perspective, niches have also been conceptualized energetically, with an ‘energetic niche’ representing the specific energy requirements or energy distributions in environments to which species are adapted (McClain et al., 2020). Adaptation to a specific niche often leads to negative density dependence with intraspecific competition negatively affecting energy balance, which prevents any one species from becoming too dominant. The second key mechanism promoting coexistence is the reduction of fitness differences among different species, which acts as an equalizing mechanism (Chesson, 2000). Individual fitness is strongly linked to energetics, since individuals will only survive if they can cover the energetic costs of maintenance, and will only reproduce if they have energy to invest in maturation and reproduction (Brown et al., 1993; Tomlinson et al., 2014). Hence, when species experience broadly similar energetic states, this may act as an equalizing mechanism slowing down competitive exclusion or, in other words, increasing the coviability of species (Jeltsch et al., 2019). In Figure 5 we summarize how energy dynamics may function as stabilizing and equalizing mechanisms and synthesize this into our overall conceptual framework.

Stabilizing mechanisms reduce competitive exclusion of species by driving stronger intraspecific density dependence, i.e., an effect of population density on population growth. For example, as populations grow, energy balance becomes negative or less positive, leading to subsequent population decreases, and vice versa (Figure 5A). This negative energy balance could be a consequence of either a positive correlation between the number of conspecifics and energy costs (caused by increases in e.g., stress, fighting, or infection), and/or negative correlations between conspecifics and energy intake (due to e.g., increased resource competition or reduced time for foraging with more time invested in interactions, Figure 5B & C). Such an overall negative density dependence of energy balance reinforces species coexistence by limiting population growth such that no single species achieves dominance.

In contrast, equalizing mechanisms can lead to similarity in energy balance among species (Figure 5D), i.e., a similar ratio of energy intake to energy costs. This can arise from scenarios where different species exhibit high energy intake matched by high costs, or low energy intake by low costs (Figure 5E), as well as cases where both energy intake and costs are similar across species. However, even when total energy expenditure is the same, there may still be differences in energy allocation to various metabolic processes (Figure 5F), which can influence fitness and coexistence dynamics.

While similarity in energy balance fosters coexistence, dissimilarity can disrupt it because species with a more positive energy balance may dominate and outcompete others. Energetics, therefore, can also have disruptive effects on coexistence. In systems initially in balance, changes in energy dynamics—such as the introduction of new resources—can reduce opportunities for coexistence. For example, human-made garbage dumps provide additional food resources, benefiting some species through increased energy intake leading to larger group sizes. As these species often still consume other resources, these larger group sizes can lead to increased competition for other species that do not exploit garbage, and to increased predation on prey species (Plaza & Lambertucci, 2017).

Despite these disruptive effects, energy dynamics offer a framework for understanding and fostering coexistence. In the following sections, we explore examples from the literature and propose pathways by which energetically mediated mechanisms can promote species coexistence.

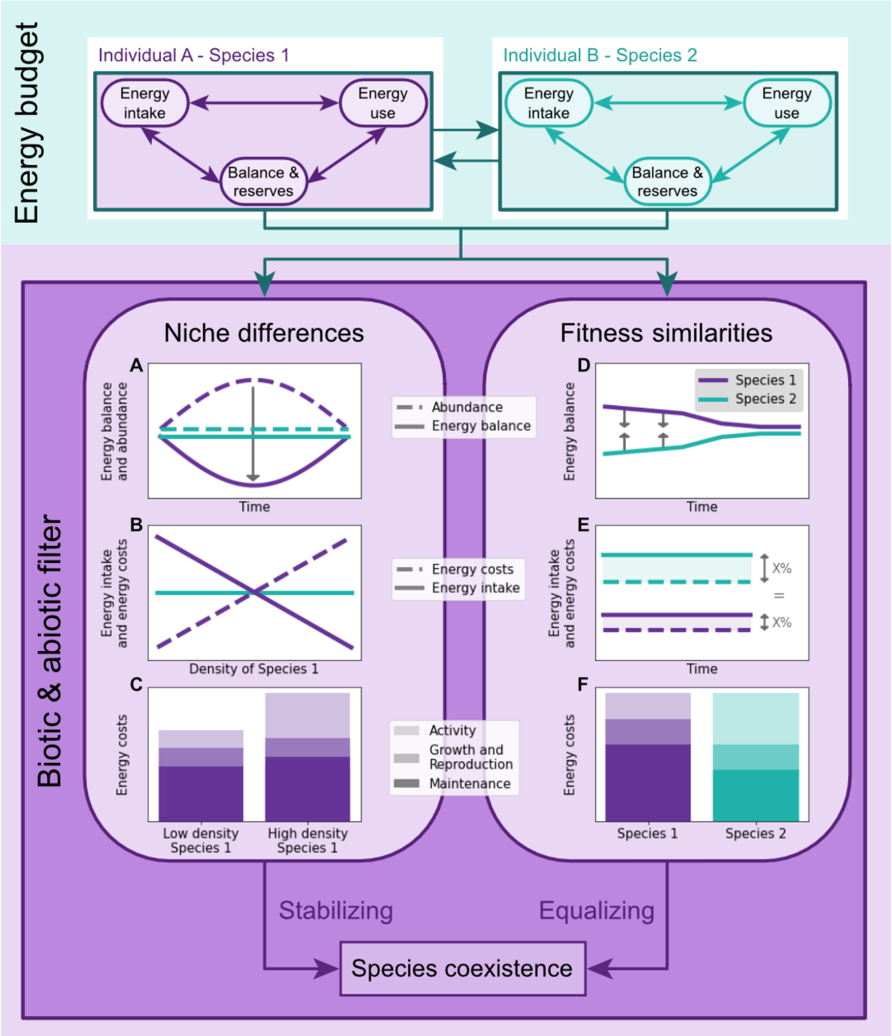

Figure 5: Conceptual visualization of how energetics may act as stabilizing or equalizing mechanisms in the context of species coexistence. When one species has a much higher energy balance, it may outcompete other species, so a stabilizing mechanism would be a reduction of energy balance with increasing abundance (A). This could occur as a result of increases in energy invested into intraspecific competition (e.g. fighting, searching for nesting sites, stress, infections) or reductions in energy intake due to intraspecific resource competition (B, C). When species have similar energy balances (incoming versus outgoing energy), they are likely to coexist due to comparable fitness (D). Similar energy balance may result even with different levels of energy intake and costs (E), and similarity in total energy costs may arise despite differences in energy allocation to metabolic processes (F).

Energy-based stabilizing mechanisms

Mechanisms that elevate intraspecific over interspecific competition include energy expenditure from fighting conspecifics (e.g., defending home ranges), stress due to high population densities (Li & Brocksen, 1977), and costs of immune activity due to increased infection rates in dense conspecific populations (Patterson & Ruckstuhl, 2013, Figure 5C). These additional energy costs can induce negative density dependence of the energy balance of individuals, i.e., negative or less positive energy balance, as population size increases (Figure 5B). Assuming that a positive energy balance leads to increased fitness and therefore dominance over species with less positive energy balance (Hall et al., 1992), this negative density dependence in energy balance would likewise reduce population growth (Figure 5A).

In the field, such an increase of intraspecific over interspecific competition may result from highly specialized energetic niches (McClain et al., 2020; Wilson et al., 2011), arising from specific energy intake requirements or adaptations in energy expenditure. An example for how specializations in energy intake can promote coexistence is seen in bee species partitioning their energetic niches through foraging efficiency (Balfour et al., 2021). Bumblebees *(Bombus spp.)*, being larger and having greater energy costs, only visited flowers offering a high energy intake-to-cost ratio, while honeybees (*Apis mellifera*) were less particular. This partitioning was driven by energy efficiency, not morphological traits like tongue or tube length and led to stronger intraspecific competition among bumblebees than between bumblebees and honeybees (Balfour et al., 2021, Figure 5B).

Another example of reduced competitive interactions during energy intake is ontogenetic niche shift, i.e., changes in the trophic niche throughout the lifespans of competing species. When a superior competitor has greater variation through its life stages in terms of energy and nutrient demands, direct interspecific competition is reduced due to trophic resource partitioning. This, in turn, can support coexistence as has been observed in the two coexisting fish species Trinidadian guppies (*Poecilia reticulata)* and killifish (*Rivulus hartii)* (Anaya-Rojas et al., 2023).

Species can also specialize in energy expenditure, e.g., by developing energy saving strategies. Such energetic strategies have been proposed to facilitate the coexistence of snowshoe hares (*Lepus americanus)* and squirrels (*Tamiasciurus hudsonicus*) in Yukon, Canada (Menzies et al., 2020). Both species are intermediate-sized, winter-active homeotherms, but they employ distinct strategies to cope with harsh winters. Hares adjust metabolically by varying their heart rate, while squirrels adapt behaviorally to minimize exposure to cold. These contrasting energetic adaptations may lead to functional and temporal niche partitioning, with activity much more dependent on temperature in squirrels than in hares. This niche partitioning can particularly mediate competition via shared predation, and influence coexistence in temporally variable environments.

Generally, energy saving strategies in periods of resource limitation, such as torpor or estivation, may effectively reduce the need to compete for resources. This could allow species to maintain population density while minimizing direct competition with other species (Levy et al., 2011).

Regarding competitive interactions, the theory of the maximum power principle posits that species with the highest metabolic rate dominate in competitive experiments and that similarly, when the summed metabolic rate of a diverse community surpasses that of a single species, coexistence may result (DeLong, 2008). This mechanism could act as a stabilizing force by enabling diverse communities with higher collective metabolic rates to outperform less diverse groups. However, we argue that a more comprehensive approach than only considering energy expenditure lies in considering energy balance, as it ultimately determines an animal's nutritional status and its ability to allocate energy to fitness-related processes.

Energy-based equalizing mechanisms

When species invest similar relative amounts of energy in survival and reproduction, this can lead to similarities in fitness, which can act as an equalizing mechanism for species coexistence (Szangolies et al., 2024). This aligns with the ‘equal fitness paradigm’, which posits that species coexist because their fitness levels are balanced through trade-offs between lifespan and reproductive investment (Brown et al., 2018; Burger et al., 2021). Hence, when species achieve comparable energy balance (Figure 5D), they may coexist, regardless of whether both species exhibit high energy intake relative to energy expenditure or similarly low values (Figure 5E).

Equalized fitness in species with differing life-history strategies, as suggested by the ‘equal fitness paradigm’, can result from trade-offs between reproductive output and somatic growth (Figure 5F). Species with a fast life-history may invest heavily in reproduction but suffer higher mortality, due to less energy investment in maintenance, e.g., the immune system. Conversely, species with a slow life history invest more energy in long-term survival and reproduce at a slower pace. Such strategies can lead to equal fitness in the long term (Brown et al., 2018). Another example is one species heavily investing into competition while another prioritizes colonizing new areas. These divergent strategies can result in comparable energy balance and overall success, reducing competitive exclusion and allowing for the persistence of several species (Pettersen et al., 2020).

Several energy-based equalizing mechanisms are strongly related to movement, directly linking activity, energy balance and the potential for species coexistence. A prominent example would be contrasting foraging modes, as also suggested by Schlägel et al. (2020). While actively searching predators have a higher chance of finding prey and thus a high energy intake, they also have high costs for movement and searching. Conversely, ambush predators that sit and wait for their prey have low movement costs, but potentially also low energy intake (Avgar et al., 2008; Scharf & Ovadia, 2006). These contrasting strategies can balance out, leading to a compensatory equalizing effect in terms of energy intake relative to expenditure (Figure 5E), with comparable resources left to allocate toward fitness-related processes.

A similar mechanism at a larger scale relates to differences between migratory and residency strategies. While migrating species or populations invest in large scale movement, often to increase their subsequent energy intake, residing species do not make this investment, but as a result may have to contend with lower resource availability (Shaw & Couzin, 2013; Shaw & Levin, 2011). Again, these contrasting strategies can result in similar energy intake relative to expenditure (Figure 5E). Along these lines, Linek et al. (2024) recently showed that total energy expenditure was relatively similar in migrating and resident common blackbirds (*Turdus merula*), but energy allocation differed substantially. While migratory birds incurred lower thermoregulatory costs in warmer wintering locations, they maintained similar long-term total energy expenditure due to an increase in energy allocation to other processes, such as fat accumulation or the growth of flight muscles, offsetting migration costs, immune function, or enhanced predator avoidance capabilities.

Similarly, Kobler et al., (2009) observed that northern pikes (*Esox lucius)* exhibiting different behavioral types coexisted by adopting distinct foraging strategies. Some pikes prioritized specific habitats while others opportunistically foraged across larger areas. The opportunistic pikes incurred higher energy costs for moving but compensated with increased foraging success, leading to equal survival of the different behavioral types (Figure 5E).

Overall, these examples demonstrate how animals with different life-history strategies and behavioral syndromes can maintain similar fitness levels by balancing energy expenditure and intake in ways that support coexistence.

What next?

The presented framework sheds new light on how the intricacies of individual energetics drive movement behaviors and shape species coexistence within communities (Figure 2). By connecting animal metabolism, movement ecology, and biodiversity research, we have emphasized a dynamic triangle of interactions and feedbacks that deepens our understanding of ecological processes. Drawing on examples from the literature, we highlight how these connections, though often implicit, have long influenced ecological theory. Our perspective integrates these insights into community ecology, suggesting that an energetics-centered approach can substantially advance our grasp of biodiversity dynamics and the far-reaching implications of global change.

To advance this conceptual framework, it is crucial to rigorously test and evaluate its predictions through a combination of experimental, field, and modeling approaches. Controlled experiments, such as classical treadmill studies, offer a promising avenue to quantify the energy costs of movement across varying speeds and contexts. Expanding these experiments to incorporate environmental complexity (e.g., incline, substrate types) or biotic interactions (e.g., virtual or physical competitors or predators) could better replicate realworld conditions. Group setups including multiple individuals of one or several species could explore coordinated movement dynamics or conflict-driven adjustments in pace and behavior, illuminating how social or competitive interactions influence energy expenditure. Additionally, variations in metabolic traits, such as basal metabolic rate, digestive efficiency, or aerobic capacity, can be assessed under differing resource availabilities or environmental conditions that drive movement, particularly using single-species and multispecies experimental setups. These studies can reveal how metabolic diversity in those traits influences species-specific adaptations and interactions, offering insights into the mechanisms that enable coexistence and resilience to environmental change.

While controlled experiments provide valuable insights, their limited environmental complexity underscores the crucial need for field studies to understand biological mechanisms in natural environments. Despite recent advances, direct measurements of energetics in dynamic, multispecies communities remain rare (but see Alton & Kellermann, 2023; Janča & Gvoždík, 2017). Field-based approaches face additional challenges due to the complexity of measuring diverse energetic variables across entire communities, yet emerging methodologies, such as bio-logging, can provide insights into movement and energetics. To examine energetics in motion, measurements like overall dynamic body acceleration (ODBA), heart rate sensors, and the doubly labeled water technique are becoming increasingly popular (Halsey et al., 2011; Wilmers et al., 2015; R. P. Wilson et al., 2020). However, these methods often capture data for only a small subset of a community, potentially limiting their broader applicability. Innovations in sensor technologies, such as multi-parameter physiological monitors for free-living animals (Williams et al., 2021), hold great promise for expanding the scope of such studies.

To complement empirical efforts, models with mechanistic underpinnings (e.g., Gallagher et al., 2021; Sibly et al., 2013; Szangolies et al., 2024; Urban et al., 2016) can integrate these insights, simulating the internal dynamics of coexisting species under varying environmental scenarios. Such models enable researchers to explore system-wide interactions that are otherwise difficult to measure. However, their success depends on high-quality data and knowledge for parameterization and validation, underscoring the need for coordinated efforts across experimental, field, and modeling studies. By combining these approaches, we can overcome existing limitations and unlock a deeper understanding of how energetics shapes and is shaped by movement and community dynamics.

Further methodological development is essential to address the complex interface between individual energy dynamics, movement behavior, and species coexistence. By encouraging collaboration between physiologists, movement ecologists, community ecologists, and ecological modellers, we aim to inspire innovative approaches that integrate physiological and behavioral measurements into multi-species analyses. Advancing this interdisciplinary effort will help answer pressing research questions and enhance our understanding of biodiversity dynamics in the face of environmental perturbations and global change.

Case studies provide a starting point for operationalizing this framework, inspiring future research. Simple systems, such as model species in laboratory experiments, demonstrate how energy dynamics respond to biotic and abiotic changes. For example, Alton & Kellermann (2023) found that activity and metabolic rates were generally higher in two-species Drosophila cultures compared to isolated populations, with energy expenditure further influenced by temperature, though this effect differed between species. Applying our framework, these findings suggest that interspecies interactions directly affect individual energetics, while temperature changes may have the potential to destabilize coexistence. Extending such studies to track long-term outcomes could address key questions about how energy dynamics mediate coexistence under shifting conditions. However, these experimental lab systems also have limitations, as they lack the complexity of natural communities and often can not account for individual energy intake, which is essential for calculating energy balances.

Field-based studies of larger species in naturally complex communities provide a complementary opportunity to explore the links between community dynamics, movement, and energetics. For instance, coexisting savanna antelope species face seasonal resource and temperature stress (Hering et al., 2022; Berry et al., 2023). Equipping individuals from multiple species in the same region with movement and physiological sensors could reveal differences in energy-budgeting strategies and behaviors, both between and within species. Linking these insights with additional tools, such as pregnancy testing and vaginal implant transmitters which monitor parturition events (as in Chimienti et al., 2020), could further illuminate the energetic mechanisms underpinning fitness and coexistence under environmental stress.

Together, such studies, whether in controlled experiments or natural settings, demonstrate the diversity of systems available to explore open questions about movement, energetics, and community dynamics. By exploring these questions across diverse contexts, future research can address the direction and strength of the links proposed in this framework, deepening our understanding of how individual-level mechanisms interact with community-level processes and drive biodiversity dynamics.

Key open questions include:

Have coexisting species evolved similar or converging energy balances, and how will these evolve under future conditions?

How do differences in energy acquisition and expenditure, such as metabolic rates and foraging efficiencies, mediate the coexistence of competing species within shared spatially and temporally variable habitats?

How does species co-occurrence influence the movement and energy dynamics of individuals, and how does this shape their responses to environmental change?

How does intraspecific trait variation in energetic traits affect variation in behavior, i.e., 'personalities' of individuals, and vice versa, and how does this relate to fitness, population persistence, or species coexistence?

How do shifts in energy resources, such as primary productivity or prey availability due to climate change, alter energetic trade-offs, movement patterns, and interspecies interactions?

How does increasing environmental unpredictability and human-induced changes challenge the energetic optimization of movement, e.g., of migratory routes and timing, particularly in multi-species assemblages, and how will this impact species coexistence?

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Conflict of interest

The authors declare no potential conflict of interests.

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