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

Leonna Szangolies*[1], Florian Jeltsch[1,2], Lewis G. Halsey[3], and Cara A. Gallagher[4]

* Corresponding author, szangolies@uni-potsdam.de

[1]University of Potsdam, Potsdam, Germany

[2]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

[3]Roehampton University, London, United Kingdom

[4]Aarhus University, Roskilde, Denmark

Abstract

To counteract ongoing biodiversity loss due to global change, we need a deeper understanding of when and how species coexist. Recent work has begun to uncover mechanistic links between species coexistence and the movement of individual animals, revealing how individual behaviour can shape community dynamics. This movement behaviour is both motivated by and constrains an animal's energy state, which in turn drives organism fitness and species interactions, for example by minimizing energy costs or maximizing energy intake. Advancing our understanding of individual energetic mechanisms can therefore reveal key drivers of coexistence. Here, we propose a conceptual framework linking animal energetics, movement behaviour and coexistence to explore how energy fluxes drive movement, mediate species interactions and shape community dynamics, extending former theories that address subsets of these relationships. Energetics is an important process influencing whether, how, where and when animals move, and underpins both equalizing (e.g., similar energy balances among species) and stabilizing (e.g., energy costs that limit large populations) mechanisms of coexistence. By synthesizing insights from community ecology, movement ecology and ecophysiology, we highlight how the integration of these fields reveals a fundamental set of interconnected mechanisms shaping species coexistence. We advocate for this mechanistic framework to improve our understanding of diversity dynamics and predictions of the impacts of environmental change on coexistence and biodiversity. We call for the development of interdisciplinary methods to test predictions evolving in this area and provide examples of how this framework can be applied to advance understanding across varied ecological systems.

Keywords: animal movement energetics, biodiversity conservation, community theory, energy dynamics, equalizing and stabilizing mechanisms, individual-based ecology

Introduction

Understanding when and how species coexist is one of the great challenges in ecology (Chesson, 2000; Hubbell, 2001; Hutchinson, 1978). 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 in insect communities (an equalizing mechanism, e.g. Hood et al., 2021) or prey switching by zooplankton feeding on phytoplankton (a stabilizing mechanism, e.g. Vallina et al., 2014). These mechanisms are often mediated by animal movement, for instance different foraging movement strategies may lead to encounters with different prey species, facilitating resource partitioning (Nakano et al., 1999), and both intra- and interspecific variation in movement behaviour can play an important role in shaping coexistence patterns (Milles et al., 2020; Rohwäder et al., 2024). This connection between movement and species coexistence has been established in previous work (Schlägel et al., 2020), but movement data alone—without a mechanistic understanding of its causes and consequences—often fails to accurately predict coexistence patterns (e.g., Costa-Pereira et al., 2022).

Other concepts seek to explain species coexistence by the physiology and metabolic rates of individuals. For example, the metabolic theory of ecology (MTE, Brown et al., 2004) uses metabolic scaling laws to explain ecological patterns across levels of organization. MTE can effectively predict life history traits of individuals, population growth rates and species interactions based on relative metabolic demands, body sizes and temperature-dependent resource utilization efficiencies (Brown et al., 2004). However, MTE largely overlooks individual behaviour and plasticity, for example in movement. Similarly, the Pace-Of-Life syndromes (POLS) hypothesis suggests that animal life-history and physiological traits co-vary along a fast-slow continuum (Ricklefs & Wikelski, 2002), promoting niche partitioning and coexistence. Its extension, the extended Pace-Of-Life syndrome (EPOLS) hypothesis incorporates behavioural traits including movement, acknowledging their role in shaping life history, physiology and ultimately coexistence (Dammhahn et al., 2018). However, these theories remain largely trait-based, emphasizing species-level patterns over individual-level behaviour and underlying physiological mechanisms.

Empirical findings indeed suggest that individual energetics can act as stabilizing or equalizing mechanisms for coexistence. For instance, differences in energy-related foraging strategies between bumblebees (*Bombus spp.*) and honeybees (*Apis mellifera*) lead to resource partitioning and reduced interspecific competition, supporting stable coexistence (Balfour et al., 2021). In common blackbirds (*Turdus merula*), variation in strategies within the species may be maintained through an equalizing mechanism that balances fitness outcomes: migrants and residents allocate energy differently but maintain similar total expenditures (Linek et al., 2024). These examples demonstrate that integrating individual-level behaviour and energetics into coexistence theory offers a mechanistic and quantifiable foundation for understanding species interactions and predicting community responses to environmental change.

Energetics encompasses both the energy available in the landscape and an individual's energy demands and reserves. 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 can shape an individual's decisions (Halsey, 2016; Shepard et al., 2013). The costs of moving around are not trivial and depend on various factors, including the landscape (e.g., terrain), the individual animal’s state (e.g., mass, reproductive state, or fat storage), their movement mode (e.g., flying, swimming), characteristics (e.g., speed) and strategy (Klarevas-Irby et al., 2021), and the presence or absence of other individuals moving similarly (i.e., collective motion; Zhang & Lauder, 2023). Since energy represents a fundamental currency of life necessary for survival and reproduction (Burger et al., 2021), the balance between energy gains and expenditure plays a crucial role in determining whether, how, where and when an animal decides to move.

In this article, we aim to describe the mechanistic triangle of interactions among animal energetics, movement behaviour and species coexistence (Figure 1). Specifically, we present a detailed conceptual framework illustrating the processes that link these domains, which enables quantitative predictions. We begin by clarifying terms from the different fields in the glossary, setting the stage to explore mechanisms linking each pair of concepts: coexistence and movement, coexistence and energetics, and movement and energetics. Although we examine the interactions in pairs, we emphasize that these are not isolated links. Rather, they represent interconnected pathways within a single mechanistic framework, with many examples inherently integrating all three elements of the triangle. With this foundation, we propose future research directions to further advance ecological theory and enhance biodiversity conservation.

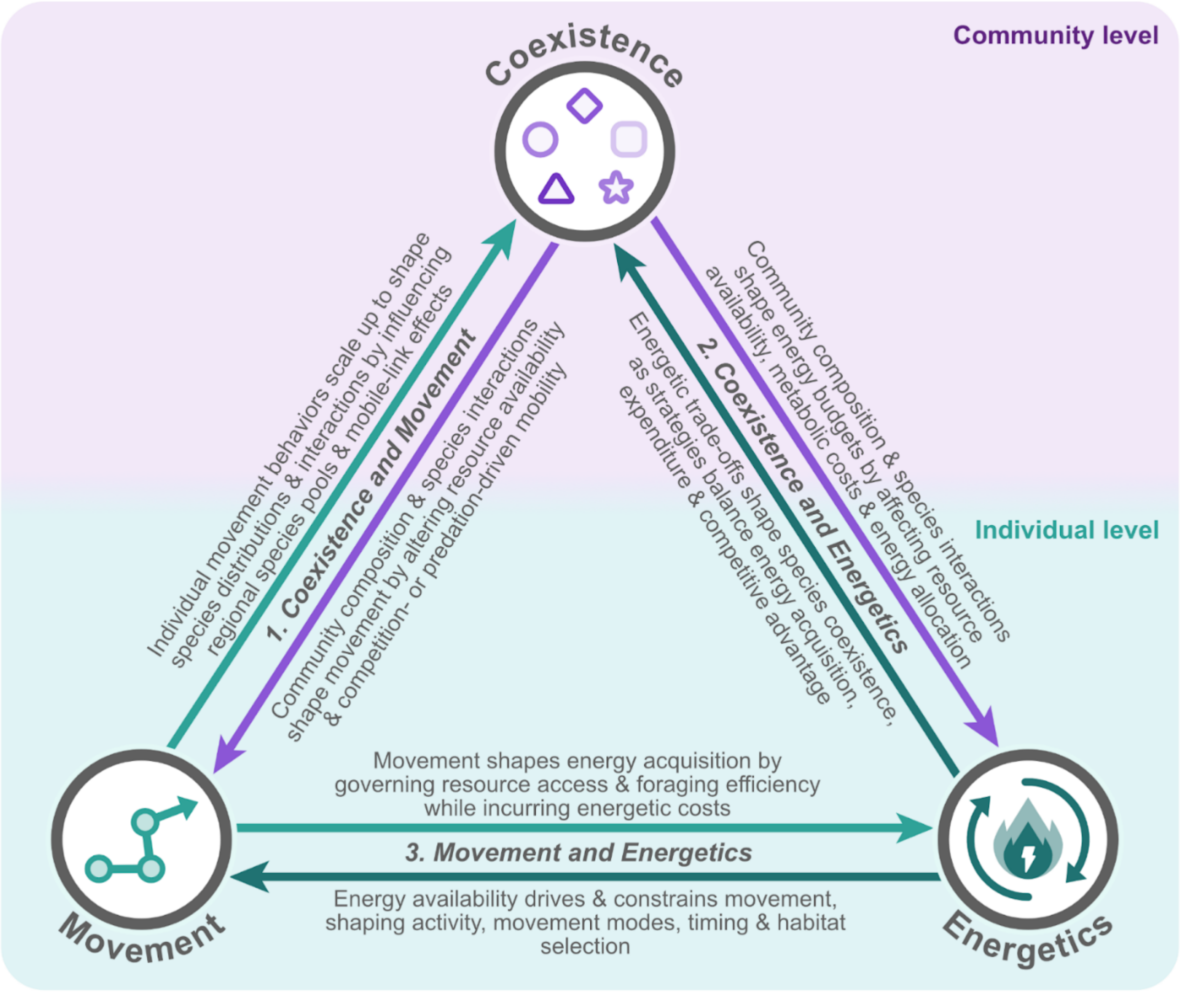

Figure 1: *Triangle of interactions among animal energetics, movement and coexistence. Brief descriptions of the links are given along the directive arrows which indicate interactions.*

Energy balance: The relationship between energy intake and energy expenditure (Caballero et al., 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 et al., 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).

Biodiversity: The variety of life across all levels of biological organization, including diversity within species (e.g., phenotypic variation), between species, and across ecosystems (UNEP, 1992). In this context, we focus specifically on the diversity of species and phenotypes that co-occur in a given area.

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, 2000).

Community assembly: 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.

Metacommunity: Concept describing a larger-scale regional species pool that is a set of communities, and is maintained through different mechanisms, for example, dispersal (Leibold et al., 2004).

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).

Movement behaviour: Emergent dynamics of spatial relocation of individuals that can be evolved and species-specific or plastic in response to environmental conditions.

Box 1: *Glossary*

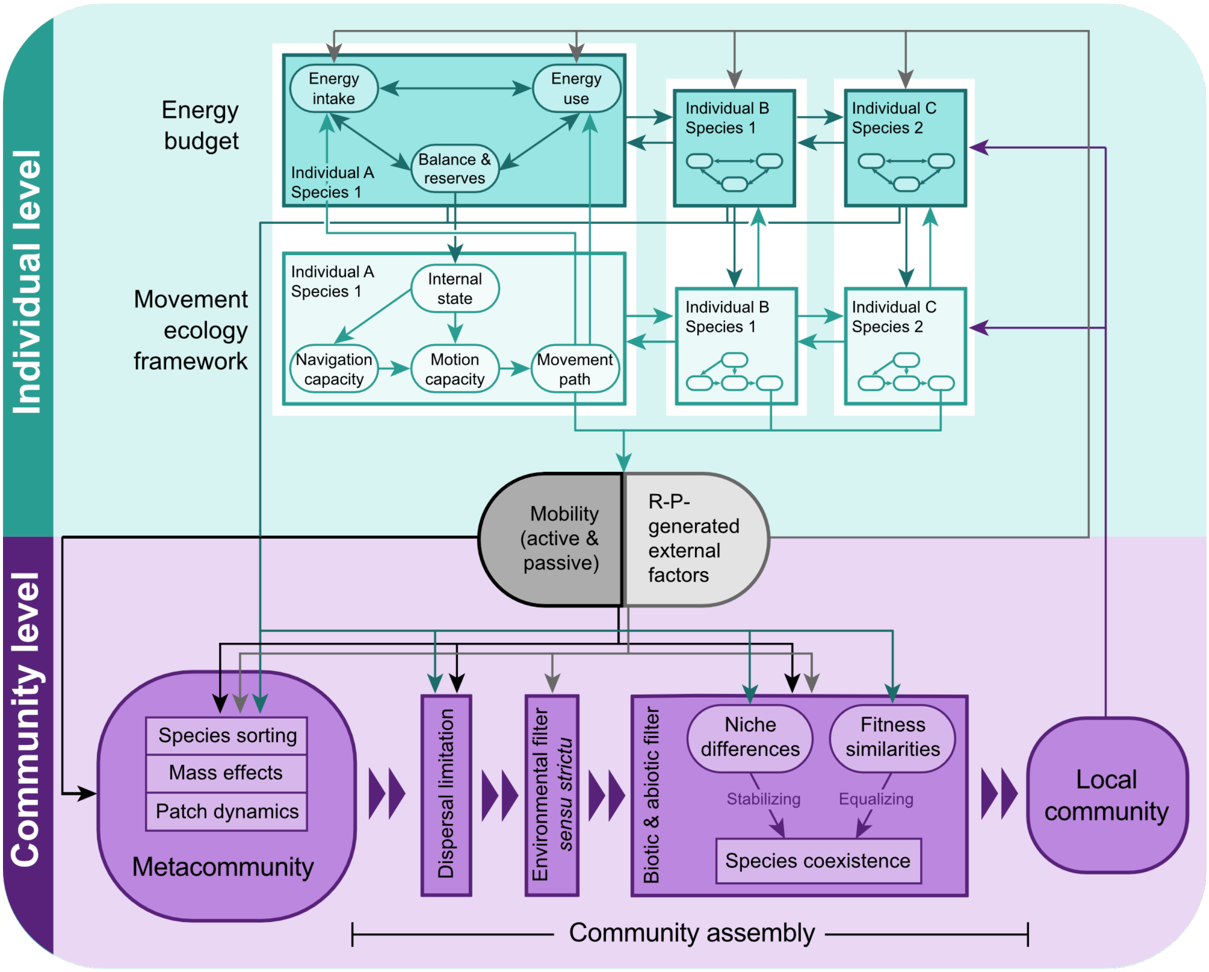

***Figure 2:** Conceptual framework linking energy budget theory with the movement ecology framework at the level of the individual animal, and integrating concepts from metacommunity theory, community assembly and coexistence theory at the community level. Movement (in light teal) and energetics (in 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 include energetics.*

An integrated framework for energy-driven movement and coexistence

We present a framework that positions individual energetics as a mechanistic basis for species interactions and coexistence, and energy budgets as the central currency driving movement decisions, from routine foraging to long-distance relocation (Figure 2, see Glossary in Box 1 for definitions). This framework details the interactions given in the triangle (Figure 1) and unifies previously parallel research tracks (e.g. linking movement to coexistence, or movement to energetics) into a cohesive set of mechanistic pathways. By explicitly tracing how energy intake and expenditure shape when, where and how animals move, and how those movements feed back into energetics and biotic and abiotic filters, this framework goes beyond former theories. It reveals new feedbacks among energy constraints, movement strategies and competition and coexistence, providing a more integrated basis for understanding and predicting coexistence patterns in a changing world.

As animals move through their habitats, they acquire energy through foraging, which is ingested, digested and stored. Simultaneously, they expend energy on life processes, collectively termed *field metabolic rate* or daily *energy expenditure* (Nagy, 1987). The balance between energy intake and expenditure, an animal's *energy balance* (see Glossary), can be positive, neutral or negative, determining whether reserves are built, maintained or depleted (Sibly et al., 2013). This energy balance shapes an individual's internal state, which in turn influences its movement decisions: whether to move, when and where to go and how to get there (Nathan et al., 2008). Movement itself can be energetically costly, depending on the mode, intensity, duration and environmental conditions (Halsey, 2016; Shepard et al., 2013). Thus, movement both responds to and reshapes an individual's energy landscape (Shepard et al., 2013, Figure 2: top panel).

Whether movement responses arise from short-term behavioural plasticity or from evolved reaction norms, the internal energetic state acts as a key integrator linking environmental conditions to movement effort. For example, individuals may behaviourally suppress activity in response to acute energy stress (e.g., Spiegel et al., 2013), or reduce activity through genetically encoded seasonal routines when food availability is predictably low (e.g., Grabek et al., 2019). In either case, movement patterns feed back on energetic processes (see Glossary: *Movement behaviour*).

Animals must balance their energy investment among movement, maintenance, growth and reproduction (Pontzer & McGrosky, 2022; Sibly et al., 2013), with individuals employing diverse strategies to navigate these trade-offs. Some increase movement to locate richer resources, while others conserve energy by reducing activity or entering states like torpor. These strategies can vary both between and within species, creating heterogeneity in energy budgeting that may buffer or amplify the effects of environmental conditions at population and community levels. For instance, Bright Ross et al., (2021, 2024) found that young, reproductive European badgers (*Meles meles*) were more active and had lower body condition in the following season, yet also showed lower mortality risk at a given condition, suggesting they could afford greater energetic investment without equivalent survival costs. In contrast, older individuals were less active and more conservative in their energy use. Such varied strategies can help stabilize populations facing environmental variability, and, through their impacts on species interactions, shape coexistence dynamics.

At the population level, individual movement scales up to species-level mobility, shaping how individuals of different species interact with each other and their environment. These interactions are central to *metacommunity* and community-level processes (Figure 2: lower panel, see Glossary). The 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) (Logue et al., 2011; Schlägel et al., 2020). Local communities are shaped through a process known as *community assembly* (see Glossary), in which species from a regional pool are filtered by a series of ecological filters (HilleRisLambers et al., 2012; Kraft et al., 2015). These include: (1) *dispersal limitation*, where energy reserves and mobility determine whether species can reach suitable habitat patches; (2) *environmental filtering*, where environmental conditions must align with a species' energetic and physiological needs; and (3) *biotic and abiotic filtering*, where species must withstand interactions with competitors, predators and mutualists, often shaped by underlying abiotic conditions. For example, where temperatures favor the productivity of ants, competition between species 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).

These filters are themselves modulated by energetics. For example, reaching a new habitat patch depends not just on distance, but on the animal's ability to allocate energy to travel without compromising survival. Once there, environmental conditions, such as temperature, can constrain metabolic rates and foraging efficiency. Biotic interactions, including competition and predation, are themselves also energy-mediated: the ability to outcompete others or withstand aggression depends on energy intake, storage and use.

Within this biotic filter, coexistence theory identifies two key mechanisms: *stabilizing mechanisms*, which reduce niche overlap, and *equalizing mechanisms*, which minimize fitness differences (Chesson, 2000, see Glossary: *Coexistence mechanisms*). Movement has already been recognized as a contributor to both, e.g., through dispersal-driven niche partitioning or mass effects (Jeltsch et al., 2013; Milles et al., 2020; Schlägel et al., 2020). Building on this foundation, we emphasize that these movement-driven processes are themselves shaped by underlying energetic constraints. For example, energy-mediated behavioural strategies like torpor or hyperactivity can alter competition outcomes even under otherwise similar environmental conditions.

To illustrate the interactions, trade-offs and feedbacks within this framework, consider an animal foraging to meet its energy needs. If local food sources are insufficient, energy balance declines prompting movement to new areas. This relocation incurs energy costs and must be weighed against the probability of finding richer patches. As energy stores are depleted, the animal's ability to reach distant patches is constrained (dispersal limitation).

Even when a new patch is reached, survival still depends on abiotic suitability (e.g., temperature; environmental filtering) and on biotic interactions. If co-occurring individuals use different resources (niche partitioning) or if they can achieve similar energetic outcomes and maintain comparable fitness levels (fitness similarity), coexistence is possible. These interactions, in turn, alter future energy access for all individuals, completing a feedback loop. Upon death, the animal’s stored energy becomes available to others via scavenging or decomposition, further linking energy flows across trophic levels.

By integrating energetics, movement and coexistence within a single framework, we offer a mechanistic lens to understand how individual-level processes scale up to shape community dynamics. In the sections that follow, we examine each of these links in detail (1. Coexistence and Movement, 2. Coexistence and Energetics, 3. Movement and Energetics), highlighting theory and empirical work that illuminates how energy and movement jointly govern the structure and persistence of communities.

1. Coexistence and Movement

There are several mechanisms by which the movement of individual animals influences species coexistence. These mechanisms span all types of movement, including dispersal, migration and daily foraging (Jeltsch et al., 2013; Schlägel et al., 2020). For instance, dispersal not only facilitates turnover and spatial connectivity in metacommunities (e.g., Logue et al., 2011) but also directly links to coexistence through the colonization–competition trade-off, where species differ in dispersal ability and competitive strength (e.g. Cadotte et al., 2006). Migration can induce competition both among migrants and between migrants and residents (Holdo et al., 2011), while daily foraging movements mediate competition for resources that are spatio-temporally heterogeneous (e.g. Buchmann et al., 2012; Wilson et al., 1999). Generally, the spatial distribution of individuals influences encounter rates, aggregation patterns and interaction strengths, including competition and predator-prey dynamics, making individual movement a key process structuring communities (Schlägel et al., 2020).

Beyond these direct effects, movement can also have mobile link effects, where animals transport nutrients, other organisms, propagules or genes (Lundberg & Moberg, 2003). For example, hares have been shown to act as effective mobile linkers in dispersing seeds via endozoochory in agricultural landscapes thus contributing to preserving plant species coexistence and biodiversity (Stiegler et al., 2021). Unlike abiotic vectors, animals can move nutrients against environmental gradients, for example, uphill during salmon runs or from deep waters to the surface via the "whale pump", enhancing productivity and shaping food web dynamics (McInturf et al., 2019). By responding to the nutrients they redistribute, animals also generate feedback loops and nutrient hotspots that influence local productivity and competitive interactions. For a detailed review of the mechanisms linking movement and coexistence see Schlägel et al., (2020).

Recent research has further expanded our understanding of movement-coexistence linkages, 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). While these examples highlight a growing interest in integrating movement processes into research on coexistence and biodiversity, they often focus on movement paths in an aggregated, descriptive way, lacking a more mechanistic basis of movement motivations and trade-offs. Digging into more mechanistic causes and consequences of individual behaviour will further enhance research on coexistence processes.

2. Coexistence and Energetics

Animal coexistence is fundamentally shaped by individual physiology and energetics (Brown et al., 2004; Hall et al., 1992; Ricklefs & Wikelski, 2002). Energetic demands shape species' home ranges, geographic distributions, and performance (Boratyński, 2020; Claunch et al., 2023), affecting their potential to co-occur (see Glossary). Energy availability limits how much individuals can invest in maintenance and reproduction, directly influencing fitness and competitive dynamics (Hall et al., 1992; Lotka, 1922). In turn, an organism’s internal energy status shapes its behaviour and movement patterns, with these individual-level processes scaling up to influence broader community dynamics and patterns of coexistence (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, behaviour and species interactions.

The two key mechanisms that govern species coexistence identified by modern coexistence theory can both be contextualized through the lens of animal energetics (Figure 2: lower panel, Figure 3). First, stabilizing mechanisms arise from niche differentiation, which reduces interspecific competition (Chesson, 2000). Because niches reflect the energetic and physiological needs of organisms (Tschapka, 2004), species may be seen as occupying ‘energetic niches’, which represent adaptations to particular energy requirements or energy distributions in the environment (McClain et al., 2020). Adaptation to a specific niche often results in negative density dependence, where intraspecific competition reduces energy balance and prevents any one species from becoming overly dominant.

Second, equalizing mechanisms reduce fitness differences among different species (Chesson, 2000). Since survival and reproduction depend on covering energy costs (Brown et al., 1993; Tomlinson et al., 2014), species with similar energetic states may persist longer together. This energetic similarity can thus slow down competitive exclusion and enhance species coviability (Jeltsch et al., 2019). These dynamics are summarized in Figure 3.

While similarity in energy balance can foster coexistence, dissimilarity can disrupt it. Species with higher energy intake or greater efficiency may gain a competitive advantage, potentially outcompeting others. In systems initially in balance, shifts in energy dynamics, such as the introduction of new resources, can reduce opportunities for coexistence. For example, human-made garbage dumps provide abundant food for some species, boosting their energy intake leading to larger group sizes. These species often continue to exploit other resources, increasing competition with other species that do not consume garbage and intensifying predation pressure on prey, ultimately threatening coexistence (Plaza & Lambertucci, 2017).

Despite these disruptive effects, energetics offer a powerful lens for understanding and fostering coexistence. In the following sections, we explore empirical examples and propose energetically mediated pathways that may support species coexistence.

Energy-based stabilizing mechanisms

Mechanisms that elevate intraspecific over interspecific competition can stabilize coexistence by inducing negative density dependence in energy balance (Figure 3A-C). These include energy costs associated with fighting conspecifics (e.g., defending home ranges), physiological stress due to high population densities (Li & Brocksen, 1977) and immune costs due to increased infection rates in dense conspecific populations (Patterson & Ruckstuhl, 2013, Figure 3C). As population density rises, energy balance declines (Figure 3B), leading to reduced individual fitness and slower population growth (Figure 3A).

In the field, an increase in intraspecific over interspecific competition can arise from highly specialized energetic niches (McClain et al., 2020; Wilson et al., 2011). For example, foraging specialization can reduce overlap in energy use and promote coexistence. In a study of bees, bumblebees, being larger and having higher energy demands, only visited flowers offering a high energy intake-to-cost ratio, while the smaller honeybees were less particular, reducing direct competition between the species (Balfour et al., 2021, Figure 3B).

Ontogenetic niche shifts—changes in trophic niche across life stages—offer another path to stabilization. When a dominant competitor's energy and nutrient demands vary substantially over its lifespan, direct interspecific competition can be reduced through trophic resource partitioning. This, in turn, can promote coexistence, as observed in two coexisting fish species: the Trinidadian guppy (*Poecilia reticulata*) and the killifish (*Rivulus hartii*) (Anaya-

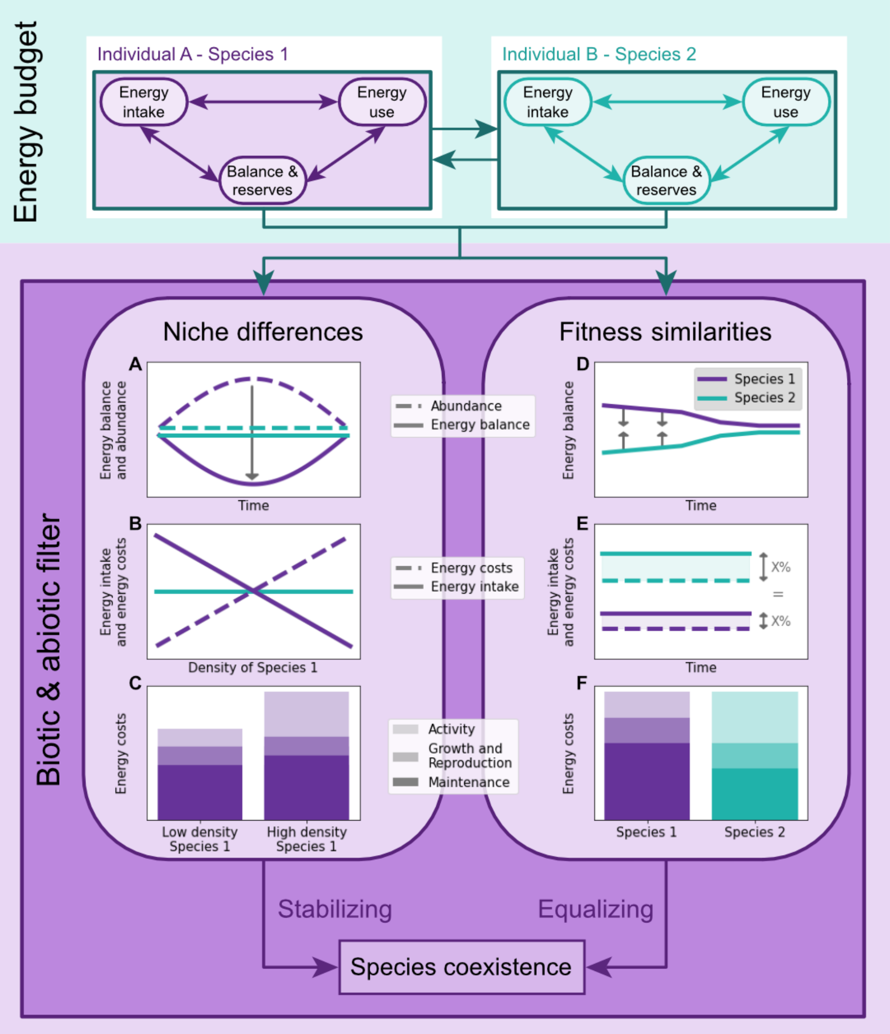

Figure 3: *Conceptual visualization of how energetics may act as stabilizing or equalizing mechanisms in the context of species coexistence. When one species has a much higher energy balance, it may outcompete other species, so a stabilizing mechanism would be a reduction of energy balance with increasing 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).*

Rojas et al., 2023).

Additionally, energy-saving strategies under resource limitation or in harsh environments can foster coexistence by reducing the need for direct competition. In the Yukon, such strategies may support the coexistence of snowshoe hares (*Lepus americanus)* and squirrels (*Tamiasciurus hudsonicus*) (Menzies et al., 2020). Although both are intermediate-sized, winter-active homeotherms, hares and squirrels use distinct strategies to cope with cold: hares adjust metabolically by varying heart rate, while squirrels rely on behavioral avoidance of low temperatures. These contrasting adaptations lead to functional and temporal niche partitioning, with squirrel activity more temperature-dependent than that of hares. This partitioning helps mediate shared predation and supports coexistence in seasonally variable environments.

Building on this, 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, rather than only considering energy expenditure, we argue that a more comprehensive approach 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

Equalizing mechanisms reduce average fitness differences between species, thereby slowing exclusion and allowing coexistence to persist even in the absence of strong niche partitioning (Chesson, 2000). In energetic terms, this can occur when species differ in how they acquire, invest, and conserve energy, yet arrive at similar net energy balance, leading to comparable fitness outcomes despite distinct ecophysiological strategies (Figure 3D–F)(Szangolies et al., 2024).

This principle aligns with the ‘equal fitness paradigm’, which posits that trade-offs between survival and production lead to balanced fitness outcomes across species (Brown et al., 2018; Burger et al., 2021). Hence, when two species achieve comparable energy balance (Figure 3D) they may coexist, regardless of whether both species exhibit high energy intake relative to energy expenditure or similarly low values (Figure 3E).

Equalized fitness can arise from trade-offs between reproductive output and somatic growth (Figure 3F), with fast-paced species investing heavily in reproduction and maintaining fitness through high turnover, while slow-paced species may achieve comparable fitness through greater longevity and lower metabolic costs. Such trade-offs result in long-term fitness parity despite contrasting energetic strategies (Brown et al., 2018).

However, environmental context can influence which energy allocation strategies are advantageous. In highly seasonal environments, fast life-history strategies may be more successful. For example, Yanco et al. (2022), using a metabolic model and global metabolic data, found that life-history diversity declined with increasing resource seasonality, suggesting that fast-paced species were favored under such conditions. Similarly, Youngflesh et al. (2025) reported that among non-migratory, non-marine birds, fast-paced species dominated in areas with high intraannual temperature variability, whereas slow-paced species were more successful under high interannual variability. While these POLS-based findings offer insight into how metabolic traits shape the coexistence of different life-history strategies, they do not fully explain variation in species survival. For instance, Boyce et al., (2020) found that songbird survival also varied with latitude, highlighting the need to explore additional physiological and ecological mechanisms underlying global life-history diversity.

Several energy-based equalizing mechanisms are closely tied to movement, linking activity patterns to energy balance and the potential for species coexistence. A prominent example is contrasting foraging modes (Schlägel et al., 2020): active predators gain more energy through more frequent prey encounters but incur high movement costs, while ambush predators conserve energy by remaining stationary but may have lower intake (Avgar et al., 2008; Scharf & Ovadia, 2006). These contrasting strategies can balance out, leading to a compensatory equalizing effect on energy balance (Figure 3E), with comparable resources left to allocate toward fitness-related processes.

A similar equalizing mechanism at a broader scale involves differences between migratory and resident strategies. Migratory species invest in large-scale movement, often to access more abundant resources, while resident species avoid these costs but may face lower resource availability (Shaw & Couzin, 2013; Shaw & Levin, 2011). Again, these contrasting strategies can result in similar energy balance and fitness (Figure 3E). In migrating and resident common blackbirds, Linek et al. (2024) recently found that total energy expenditure was relatively similar across strategies, 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 3E).

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

3. Movement and Energetics

The relationship between energetics and movement (Figure 2: top panel, Figure 4) offers a mechanistic lens into how individual activity scales up to influence communities and coexistence. Energy from metabolic processes fuels locomotion (Figure 4A), and while movement can substantially raise daily energy expenditure (Halsey, 2016), mobility enables access to remote or ephemeral resources, shaping how animals interact with their environments and one another. Scientific interest in the links between locomotion and energy use dates back over 125 years (e.g., Zuntz, 1897) and advanced rapidly with the development of respirometers in the 1970s (Garland, 1983; Schmidt-Nielsen, 1972; Taylor et al., 1970). Today, animal-attached bio-logging devices can provide precise measurements of proxies of activity and energy expenditure in wild animals (Fahlman et al., 2021; Wilmers et al., 2015). However, there has been much focus on measuring locomotion costs, with relatively less attention given to the physiological mechanisms driving movement behavior (but see Hetem et al., 2025). Recent studies have begun to explore the connections between physiology, short-term activity, exploratory behavior and dispersal, revealing an intricate interplay between an animal's internal state and its movement strategies (Wu & Seebacher, 2022). We here highlight the drivers and consequences of animal decision-making around the fundamental questions of why to move, how to move, and when and where to move (Nathan et al., 2008, see Glossary: *Movement ecology paradigm*), describing how these decisions reverberate across ecological scales.

Why move: Energetic triggers and consequences for coexistence

Energy serves as both a motivator for and a cost of movement. Foraging movements provide energy but incur costs associated with locating, obtaining and digesting resources (Figure 4). Animals must forage 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 4). For example, 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 5A). However, this strategy came with the trade-off of increased predation exposure (Denryter et al., 2024). Hunger and other stressors can alter movement through hormonal pathways, as the production of stress hormones like glucocorticoids can alter foraging effort and risk tolerance (Creel et al., 2013; Goossens et al., 2020).

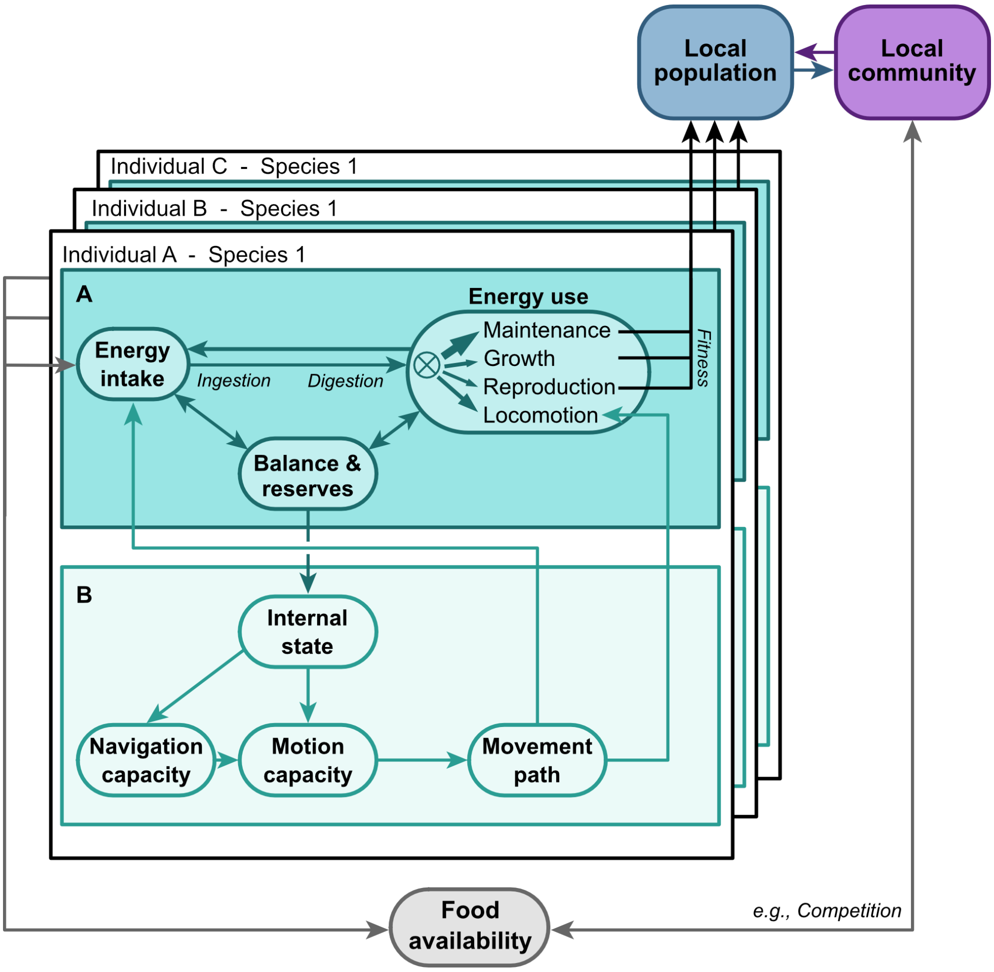

Figure 4: *Integrating individual energy budgets (A) with movement decisions (B) and their effects on population and community dynamics. An animal acquires energy from its environment through foraging movements (light teal arrows), then allocates ingested energy to digestion, maintenance, locomotion, growth, and reproduction. The resulting balance and reserves define its internal state, which in turn drives decisions about whether, how, when and where to move. Movement paths both determine future energy intake, by selecting patches with particular food availability, and incur locomotion costs that trade off against other metabolic demands. Arrow thickness in the "Energy use" panel provides an illustrative snapshot of potential allocation among processes, and light teal arrows highlight the feedback loop between movement and energy balance. Positive energy balance allows storage of surplus reserves for later use. Changes in energetics and movement behavior shape individual fitness, influence population trajectories (dark blue), and ultimately drive local community structure (purple) through competition for resources and shifts in species' habitat occupancy. This schematic emphasizes the key pathways by which energy fluxes and movement interact to mediate species interactions and govern coexistence under variable environmental conditions.*

Yet, as previously noted, in some contexts conserving energy by reducing activity may be more beneficial than seeking food (Denryter et al., 2021; Spiegel et al., 2013). For example, griffon vultures (*Gyps fulvus*) exhibit a flexible, hump-shaped response to hunger, increasing movement at moderate food deprivation levels but reducing it as starvation risk grows, suggesting a strategic shift from food-intake maximization to energy-expenditure minimization (Spiegel et al., 2013). Torpor, hibernation and aestivation allow animals to endure unfavorable conditions by lowering metabolic rates (Staples, 2016). For instance, house mice (*Mus musculus domesticus*) exhibit increased torpor in response to higher foraging costs (Schubert et al., 2009), while the marsupial Monito del monte (*Dromiciops gliroides*) responds to chronic calorie restriction by increasing torpor frequency (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*), for example, double their body mass and triple their fat stores before hibernation (Kenagy & Barnes, 1988). In such cases, movement facilitates future energy conservation.

Thermoregulation also shapes movement behavior. Increased movement can help offset hypothermia (Humphries & Careau, 2011), while movement may be reduced to avoid overheating (Dyer et al., 2023; Speakman & Król, 2010; Trondrud et al., 2023, Figure 5A). However, heat responses may vary by species. In three coexisting African antelopes—springbok (*Antidorcas marsupialis*), greater kudu (*Tragelaphus strepsiceros*) and common eland (*Tragelaphus oryx*)—behavioral responses to heat stress were shaped by differences in body size, habitat use and mobility (Berry et al., 2023).

Internal energy state is thus central to movement decisions (Figure 4). Fatigue, digestion, pregnancy and disease all affect energy intake and allocation, influencing when and whether to move (Birnie-Gauvin et al., 2023; Kramer & Mclaughlin, 2001; van Hoven & Boomker, 1985; Gleiss et al., 2019; Dayananda et al., 2017; Noren et al., 2012; Binning et al., 2017; Grabow et al., 2024). Life history strategies and predation avoidance behavior further influence these energetic trade-offs.

The decision to move or stay is shaped by the balance between energy reserves, physiological needs, and environmental risks. From routine foraging to long-distance dispersal, these decisions reflect dynamic thresholds: animals may delay leaving shelter until energy stores fall below a certain level, shorten foraging bouts under scarcity or increase movement to prepare for future energetic demands (Penteriani et al., 2022; Speakman, 2014; Spiegel et al., 2013). These state-dependent rules stagger when and where individuals are active, reshaping patterns of space use and altering the timing of interactions. As a result, even in shared environments, species can reduce direct competition and coexist. Framing coexistence through the lens of internal energy dynamics shifts the focus from static resource availability to the flexible, condition-dependent rules that govern movement. It is not just how much energy is available but how and when animals decide to pursue it that can determine who persists in fluctuating environments.

How to move: Movement strategies, trade-offs and species interactions

The energetic costs and benefits of movement depend on how animals navigate their environments (‘motion capacity’, Figure 4). Fast pace-of-life species, with high metabolic rates and early reproduction, often use energy-intensive, high-speed movement (e.g., migratory birds and mammals; Soriano-Redondo et al., 2020; Winger & Pegan, 2021). In contrast, slower strategists may favor passive or low-cost locomotion, trading range for energy conservation. Passive modes like gliding or drifting save energy but reduce control, limiting access to reliable resources. Active modes, like running, flying and swimming, offer greater control and reach but come with higher energy costs. Walking and running have a lower cost per unit time, while flying and swimming are more efficient per unit distance (Schmidt-Nielsen, 1972). However, increases in speed raise costs steeply in swimming and flying, while running costs rise more linearly (Hedenström & Alerstam, 1997; Heglund et al., 1982; Hind & Gurney, 1997).

Species capable of multiple movement modes often face trade-offs. For example, in starlings (*Sturnus vulgaris*), experimental studies have shown that individuals switch between walking and flying, weighing locomotion costs against foraging efficiency to maximize net energy gain per unit time (Bautista et al., 2001). Similarly, in the Southern Beaufort Sea, some polar bears (*Ursus maritimus*) have shifted from sea ice to land in response to ice loss (Pagano et al., 2020). These land-bound bears swim more and expend more energy, but gain access to higher-quality foraging areas, potentially offsetting their increased locomotion costs (Pagano et al., 2020). Such cases highlight how animals adjust movement strategies to balance energy expenditure with resource access.

Different movement types reflect varying strategies for energy management. Station-keeping and home ranging movements allow animals to remain near stable resources, but even routine movements can be costly (Boratyński, 2020). Home ranges may also require defense, adding further energetic demands (Ord, 2021). Dispersal can be triggered by deteriorating local conditions and the need to locate new resources or habitats (Matthysen & Clobert, 2012; Ronce, 2007). While dispersal can reduce competition and increase access to resources, it involves energetic costs for travel and exploration (Benoit et al., 2020) and may reduce foraging opportunities until a new site is found (Zollner & Lima, 2005). Some species reduce costs by adopting straighter, faster dispersal paths, as in transient vulturine guineafowl (*Acryllium vulturinum*, Klarevas-Irby et al., 2021). Still, dispersal may be triggered even in energetically compromised individuals when competition intensifies (Baines et al., 2020; Barbraud et al., 2003; Bonte & De La Peña, 2009; Goossens et al., 2020).

Migration for many species is driven by predictable, seasonal shifts in energy availability (Milner-Gulland et al., 2011). While the decision to migrate may balance energetic trade-offs, the act of migration itself can require precise physiological and behavioral preparation. Long-distance travel demands substantial energy, often met through premigratory hyperphagia or the use of stopover sites for refueling (Odum, 1960; Zimin et al., 2023). Nomadic strategies help animals exploit unpredictable, patchy or ephemeral resources (Stratmann et al., 2021; Teitelbaum & Mueller, 2019). For instance, in the Australian desert, banded stilts (*Cladorhynchus leucocephalus*) undertake remarkably long and rapid continent-wide movements to track ephemeral wetland resource pulses critical for breeding (Pedler et al., 2014, Figure 5B). Such movements highlight the challenges faced by fully nomadic species, as their need for near-constant motion in search of unreliable resources (Teitelbaum & Mueller, 2019) can make nomadism both energetically costly and risky.

Expanding niche theory to include how animals move, and at what energetic cost, also offers insight into species coexistence. Movement efficiency influences how far individuals can travel to access resources and how frequently they must move to meet energy demands. For example, species that glide or drift may traverse larger areas with minimal cost, while those using short, intense bursts of activity may be constrained to high-quality, localized patches. These differences can reduce spatial and temporal overlap, even among species with similar resource needs, thus easing competition.

When and where to move: Navigating energy landscapes and shaping community structure

An animal’s decisions about when and where to move are shaped by its energetic state and by current or anticipated resource availability (‘navigation capacity’ in Figure 4). These decisions span temporal scales, from rapid behavioral adjustments to seasonal strategies. Diel movement patterns, for instance, often reflect energy management. Dogfish (Scyliorhinus canicula) migrate vertically each day, moving from cold, deep resting waters to warmer, shallower foraging areas (Sims et al., 2006). Juvenile coho salmon (Oncorhynchus kisutch) feed in cold, prey-rich waters, then move to warmer areas to accelerate digestion and growth (Armstrong et al., 2013, Figure 5C). However, weather conditions and extreme events can disrupt these finely tuned routines, limiting daily movement and foraging opportunities, and altering costs of transport (Bradarić et al., 2020; Denryter et al., 2021; Semenzato et al., 2021, 2021; Sheppard et al., 2021).

Seasonal movements are often timed through a combination of external cues (e.g., photoperiod, temperature) and internal mechanisms (e.g., fuel stores, corticosterone levels, circannual rhythms, e.g., Eikenaar et al., 2018; Fudickar et al., 2021, Figure 5C). These strategies often align with predictable resource dynamics (Abrahms et al., 2021). For example, herbivores may ‘surf the green wave’ of vegetation phenology to optimize energy intake as resources emerge (Bischof et al., 2012; Hering et al., 2022). In the Greater Yellowstone Ecosystem, elk (Cervus elaphus) that more closely tracked spring green-up accumulated greater fat reserves by autumn (Middleton et al., 2018).

Hence, the paths animals follow and how they distribute themselves in space reflect a balance between energy gain and the costs of moving through heterogeneous terrain, vegetation, and microclimates. (Klappstein et al., 2022; Shepard et al., 2013; Wilson et al., 2012). While animals often rely on immediate cues (e.g., scent, temperature) to decide when and where to move, spatial memory enables them to return to previously profitable areas (Abrahms et al., 2019; Collet et al., 2025). However, under shifting conditions, reliance on memory may become maladaptive. 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 conditions change rapidly (Abrahms et al., 2019). In reality, animals likely integrate proximate cues, intrinsic factors, and memory to guide movement in order to manage their energy balance (Merkle et al., 2019).

Decisions about when and where to move, such as ‘surfing green waves’, shifting to thermal refuges or timing migrations, do more than optimize individual energy budgets. They shape spatiotemporal overlap among species, filtering competitive and facilitative interactions. By navigating energy landscapes, animals self-organize into distinct niches: some gain a competitive edge by tracking resource peaks, while others reduce overlap by shifting in time or space. These energetically informed strategies not only reflect how animals balance energy gain and expenditure across dynamic environments, but also influence how communities are structured.

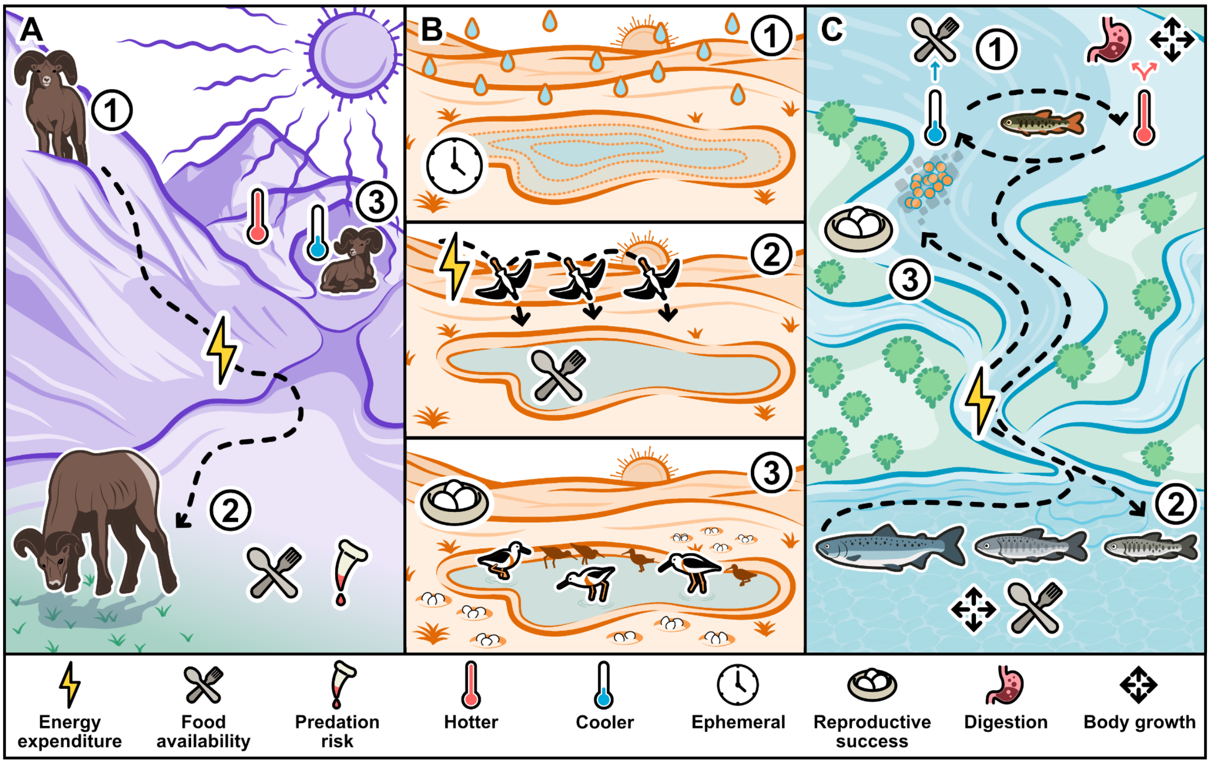

Figure 5: *Examples of how energetics shape decisions about whether to move (A), how to move (B), and when and where to move (C). In Sierra Nevada bighorn sheep (Ovis canadensis sierrae), individuals with higher energy reserves remain at high elevations to conserve energy (A1), while those with lower reserves migrate to access better forage, despite increased predation risk (A2) (Denryter et al., 2021). Desert bighorn sheep (O. c. mexicana) also benefit energetically from resting behaviour, using caves during midday heat to reduce thermoregulatory and water costs (A3) (Cain et al., 2008). Banded stilts (Cladorhynchus leucocephalus) exemplify energy-driven movement strategies, using long, nomadic flights (B2) to locate ephemeral, food-rich water bodies (B1) essential for reproduction (B3) (Pedler et al., 2014). Coho salmon (Oncorhynchus kisutch) illustrate scale-dependent timing and location decisions. Juveniles migrate daily between cold, food-rich habitats and warmer areas to optimize digestion and growth (C1) (Armstrong et al., 2013). After growing for a year or more, they migrate to sea when body size, abiotic factors, and food availability align (C2), then return to natal streams to spawn and 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). Icon meanings are explained in the legend below.*

Putting the framework to work: Novel predictions for coexistence under change

Our framework relies on explicit, bidirectional coupling of energy balance and movement decisions, and embeds this coupling within the stabilizing–equalizing framework of coexistence theory. When an animal's energy reserves rise or fall, its movement-rules, governing when, where and how to forage or disperse, change accordingly. Those shifts alter resource use patterns (niche differences) and set energetic limits on survival and reproduction (fitness differences). In turn, this reshapes the filters: dispersal, environmental, biotic, and abiotic; that determine which species can establish and persist in a given landscape. By tracing these pathways explicitly, we can generate concrete, testable predictions about when and how species coexist - predictions that lie beyond the reach of theories focused on energy, movement or coexistence in isolation.

We build on existing theories in several ways. The MTE and the Maximum Entropy Theory of Ecology emphasize energetic constraints across scales, while EPOLS theory links life history variation to energy use and movement (Brown et al., 2004; Dammhahn et al., 2018; Harte, 2011). Our framework progresses these concepts by explicitly coupling energy intake and expenditure to individual behaviors, specifically, movement decisions driven by internal state, and demonstrating how those decisions shape species interactions and community assembly. Without this integration, critical feedbacks remain hidden, such as how energy constraints alter movement strategies that then affect access to limiting resources and how species compete with each other.

While the full integration of all framework components is particularly novel and promising for future studies, even applying selected combinations of its elements can improve predictions about certain aspects of species coexistence. Hence, different parts of the framework may be considered depending upon the research focus. Nonetheless, maintaining a holistic view that fully integrates energetics, movement and coexistence offers a mechanistic and predictive lens for understanding how individual-level dynamics scale up to shape community structure.

Addressing methodological barriers

Operationalizing this framework requires linking individual energetics to behavior and interactions of individuals and species under realistic conditions. While tools for measuring movement, physiology, and community structure exist, integrating them remains a challenge. In the following we outline how three complementary approaches—controlled experiments, field-based methods, and mechanistic simulation modeling—can complement one another to test predictions and refine the framework.

Controlled experiments can be used to quantify the energy costs of movement or test fitness outcomes under standardized conditions. Treadmill studies, for example, can incorporate environmental complexity (e.g., slope, temperature) and biotic interactions (e.g., predators or competitors) using visual or other stimuli (e.g., Lees et al., 2013; Shemery et al., 2023). Mesocosms offer a flexible platform to measure metabolic traits (e.g., basal metabolic rate, aerobic scope) under varying resource regimes and community structures, allowing researchers to examine how physiological diversity shapes movement and interaction outcomes, as well as how social dynamics influence energy use and behavior (Levy et al., 2011; Nespolo et al., 2022).

Field-based methods are essential for capturing energy use in ecologically realistic contexts. Multi-sensor technologies recording accelerometry, heart rate and temperature, among other metrics, allow estimation of field metabolic rates (Halsey et al., 2009; Hawkes et al., 2021), though these often require calibration in laboratory settings using respirometer studies or doubly labelled water (e.g., Green et al., 2009). Although often restricted to small subsets of individuals, these approaches are becoming more scalable through innovations in tagging technologies. When combined with measures of resource availability, such as from remote sensing, they support the creation of energy landscapes (e.g., Berti et al., 2025). Machine learning applied to field data can further infer energy expenditure from movement patterns and uncover latent interaction dynamics within complex, high-dimensional ecological datasets (Pichler et al., 2020; Williams et al., 2020).

Mechanistic simulation models are essential for bridging biological scales, from individual energetics and behavior to population and community dynamics (Jeltsch et al., 2025). These models provide a powerful means to simulate how internal state variables, movement rules and energy budgets interact to shape species interactions and coexistence under changing environmental conditions (e.g., Milles et al., 2020; Szangolies et al., 2024). Unlike correlative approaches, mechanistic simulation modeling allows researchers to explore causal pathways and emergent outcomes that are otherwise difficult or impossible to observe directly. Such models are particularly valuable for forecasting responses to novel or extreme scenarios, such as climate-driven shifts in resource availability or species introductions (Daniels et al., 2023; Gallagher et al., 2022). However, their predictive power depends on high-quality empirical data for parameterization and validation, reinforcing the need for coordinated, cross-disciplinary efforts that integrate experimental, field, and modeling approaches.

By combining the different approaches, we can overcome existing limitations and unlock a deeper understanding of how energetics shapes, and is shaped by, movement and community dynamics. For example, conducting parallel experimental or field studies alongside model development can allow for the targeted measurement of parameters needed to inform models and to test model-derived predictions in real-world scenarios. 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 ecological questions and enhance our understanding of community biodiversity dynamics in the face of environmental perturbations and global change.

In the following, we highlight several illustrative testable predictions that emerge from our framework, describing how they are embedded within its structure and offering approaches for their evaluation. These predictions underscore the importance of jointly considering movement, energy and coexistence processes to understand how energy-mediated movement dynamics shape the assembly and persistence of communities in a warming, increasingly variable world.

Prediction 1. Under resource scarcity, individuals that flexibly switch between intensive foraging and energy-saving modes will persist longer than inflexible individuals, driving movement patterns that reshape competitive interactions and community composition.

In the presented framework, reduced energy intake leads to a negative energy balance, depleting reserves and altering the individual's internal state. This shift can trigger a behavioral transition from high-effort foraging to energy-saving modes. Species with this flexibility may down-regulate motion capacity under scarcity, minimizing locomotion costs and preserving energy stores. In contrast, inflexible species that maintain high movement rates under low returns may quickly exhaust their reserves, leading to higher mortality or competitive disadvantage. When resources remain accessible but patchily distributed, such persistent movement may confer short-term advantages, but under ongoing scarcity, it becomes maladaptive. By modulating movement effort according to energetic state, flexible species reduce costly encounters in the biotic and abiotic filter, reducing competition and potentially stabilizing coexistence.

This prediction is supported by studies showing non-monotonic movement responses to hunger in species such as griffon vultures (Spiegel et al., 2013), which balance foraging motivation against starvation risk, and by research on small mammals that use torpor to conserve energy and buffer periods of competition or scarcity (Levy et al., 2011; Nespolo et al., 2022; Schubert et al., 2009). While the effects of energy-saving strategies on competitive outcomes remain underexplored, recent work suggests these behaviors may mediate coexistence by reducing direct competition during resource bottlenecks (Levy et al., 2011). However, studies directly linking such strategies to energetics or fitness outcomes are still lacking.

To test this prediction, controlled manipulations of resource availability in semi-natural environments could be paired with fine-scale monitoring of movement (e.g., GPS, accelerometry), metabolic rates (e.g., heart rate loggers, doubly labeled water) and fitness outcomes (e.g., survival, reproduction). Comparative studies across species or phenotypes with varying capacities for energy conservation would reveal how state-dependent movement plasticity shapes persistence and community dynamics under resource limitation. As droughts intensify and food pulses become more erratic, species capable of shifting between high-effort foraging and low-effort conservation modes may be better equipped to track ephemeral resources and survive prolonged lean periods.

Prediction 2. In environments with fluctuating energy availability, individuals with higher energy demands or lower tolerance to deficits will move away from depleted patches more rapidly, leading to shifts in community composition.

Individuals continuously assess local energy intake relative to their internal reserves. In our framework, as energy returns decline, an individual nearing an energetic threshold may abandon its current patch in search of better conditions. Moreover, consistent with Optimal Foraging Theory and the marginal value theorem (Charnov, 1976), the net benefit of moving, defined as expected gains in a new patch minus the energetic and risk costs of travel, will modulate the energetic threshold for departure, so that longer distances or higher travel costs elevate the internal deficit at which individuals abandon depleted patches. Alternatively, individuals may attempt to build sufficient energy stores before performing costly dispersal, leading to a U-shaped relationship between body condition and dispersal probability (e.g., Barbraud et al., 2003). Importantly, species likely differ in the energetic thresholds that trigger departure. Those with higher metabolic demands, smaller energy buffers, or narrower physiological tolerances may leave depleted areas sooner than more energetically resilient competitors. This mechanism extends the classic R* rule, which suggests that in competing species the one which survives on a lower resource level will become dominant (Tilman, 1982), into dynamic, heterogeneous systems, where persistence depends not only on minimum resource needs but on energy-buffering capacity and behavioral responses to resource dynamics. Even modest species-level differences in energetic thresholds could potentially drive divergent spatial responses to shared environmental change.

Empirical work already supports components of this mechanism. For instance, Teunissen et al., (2025) found that endangered purple-crowned fairy-wrens (*Malurus coronatus*) were more likely to disperse and travelled farther from low-quality or isolated patches, but also increased dispersal distance with food availability, indicating that favorable energy conditions enable investment in costly, long-range movement. Thus, both resource scarcity and energetic opportunity can shape dispersal decisions. While the importance of condition in dispersal behavior is generally widely acknowledged (e.g. Bonte & De La Peña, 2009), interspecific variation in these processes due to differences in metabolic sensitivity and impacts on community assembly remain unexplored. Variation in metabolic demands, buffer capacity and dispersal thresholds could underlie shifts in dominance, coexistence and biogeographic sorting under environmental stress, helping explain why some species fragment, collapse or fail to recolonize a suitable habitat under climate change.

This prediction could be tested by tracking sympatric species with differing energetic demands in a shared, fluctuating landscape. In a semi-arid system with predictable dry-season declines, individuals from two or more species, which differ in metabolic rate, body size or physiological flexibility, could be fitted with GPS and energy-use sensors (e.g., accelerometers, heart rate loggers), while habitat monitoring (e.g., remote sensing) tracks resource availability. Linking movement with energy status and local conditions could reveal species-specific thresholds for patch departure. For example, if one species reliably departs sooner as conditions deteriorate it would indicate lower tolerance to declines and highlight how energetic traits shape patch abandonment. Long-term data could show how these differences influence community persistence and spatial sorting, particularly across years with contrasting rainfall. Semi-arid systems may be especially vulnerable to global change, as climate-driven drought and land-use-induced degradation make energy resources increasingly patchy and unpredictable. In response, species with high demands or narrow tolerances may face repeated, costly relocations, leading to fragmentation or local extinction, while more tolerant species may persist through bottlenecks and benefit from reduced competition. Understanding these dynamics can illuminate drivers of biodiversity shifts under increasing environmental volatility.

Prediction 3. Interference competition among sympatric species will intensify as their metabolic niches increasingly overlap.

Classic niche theory holds that the degree of resource-use overlap governs the intensity of interspecific competition, traditionally focusing on diet, habitat, and time (Chase & Leibold, 2009). Expanding the niche concept to include energetic demands (e.g., metabolic rates, energy acquisition needs) and movement traits (e.g., foraging range, speed, timing) adds a critical dimension of spatial and temporal overlap that elevates direct interference competition. When species not only consume similar resources but also similarly invest their energy, direct encounters become more frequent, escalating stress, displacement, and injury, and reducing potential for coexistence. Energetics shape both access and outcomes of interactions: they determine how far and how often individuals can move, and how effectively they compete when encounters occur. Thus, even energetically efficient species may suffer under high overlap in metabolic niches due to frequent, costly interactions. By contrast, differences in energy budgets or activity timing can reduce encounters through spatial, temporal or energetic partitioning, weakening interference and facilitating coexistence.

Support for this prediction comes from studies showing that similarity in energetics can intensify antagonism, for instance, bacteria more strongly inhibit metabolically similar competitors (Russel et al., 2017). In ground beetles, warming experiments revealed that *Pterostichus melanarius* (with a weaker metabolic response to temperature) exhibited stronger interference at higher temperatures, while *Poecilus versicolor* (with greater metabolic sensitivity) prioritized foraging over aggression (Lang et al., 2012). These studies suggest that similarity in metabolic and movement traits can magnify interference, while differences may buffer it. However, empirical links between these dynamics and long-term fitness or coexistence outcomes are lacking.

To test this prediction, spatially explicit individual-based models (e.g., Szangolies et al., 2024) could assign to species or phenotypes distinct metabolic rates and corresponding movement rules (e.g., foraging speed, search radius, timing). When individuals co-occur in a patch, an interference event could be triggered, scaled by the similarity of metabolic rates and movement traits. By simulating gradients of metabolic–movement overlap (low to high), one could track encounter frequency, conflict duration, energy loss and resulting survival or reproduction. Comparing outcomes under stable versus variable resource regimes could clarify how energetic overlap drives interference and alters coexistence potential. Such models could also predict outcomes for novel assemblages, including invasive species, where increased niche overlap might intensify conflict under climate warming or resource scarcity.

Conclusion and implications for dynamic communities under global change

Global change is reshaping energy landscapes. Land use change, droughts, heatwaves, resource pulses, and invasions increasingly alter not just resource availability, but the energetic costs of acquiring them. Species must continually adjust their movement strategies and interactions to track a shifting energetic terrain. The proposed framework offers a perspective for anticipating how these adjustments propagate across different scales.

Energetic mismatches may accelerate species turnover by filtering out individuals that cannot meet metabolic demands. Interaction networks may reorganize as movement patterns change, producing novel spatial and temporal overlaps, and previously unobserved assemblages. These transitions are likely to not be gradual. Thresholds may be crossed when energetic constraints are breached, triggering abrupt shifts in movement, competition or coexistence outcomes.

Addressing these challenges requires integrating across scales, from individual traits and behaviors to population and community dynamics. Trait-based approaches remain valuable but must be paired with process-based models that capture how energy fluxes and movement strategies respond to environmental variability. Embedding these processes within coexistence theory can help build a more mechanistic and predictive ecology of biodiversity under change.

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Conflict of interest

The authors declare no potential conflict of interests.

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