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Applications and implications of ecological energetics

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Abstract: 120 words

Text: 3685 words

Text Boxes: 3 (393, 400, 397 words)

Figures: 1

Tables: 1

References: 100

25 **The ecological processes that are crucial to an animal's growth, survival and reproductive**
26 **fitness have energetic costs. The imperative for an animal to meet these costs within the**
27 **energetic constraints of the environment drives many aspects of animal ecology and**
28 **evolution, yet has largely been overlooked in traditional ecological paradigms. The field of**
29 **'ecological energetics' is bringing comparative physiology out of the lab and, for the first**
30 **time, is becoming broadly accessible to field ecologists addressing real-world questions at**
31 **many spatial and temporal scales. In an era of unprecedented global environmental**
32 **challenges, ecological energetics opens up the tantalising prospect of a more predictive,**
33 **mechanistic understanding of the drivers of threatened species decline, delivering**
34 **process-based modelling approaches to natural resource management.**

35

36 ***Predicting species responses to rapid environmental change***

37 The 'Anthropocene' has become associated with rapid environmental change, not
38 only in global land use and climate [1, 2], but in biodiversity, ecological stability and the
39 ecosystem services on which humans depend [3]. The pace of change challenges our ability
40 to understand shifting patterns of biotic interactions between species and their
41 environment, and predict how these changes will influence conservation managers and
42 environmental decision-makers into the future. Repeated calls have been made for more
43 predictive, process-based approaches to modelling species' responses to global
44 environmental challenges (e.g. [4, 5]), yet limited progress has been made on this front in
45 most areas of ecology or environmental impact assessment [6].

46 Arguably one of the most neglected factors in conservation management is a
47 mechanistic understanding of the energetic requirements of an organism, and how those
48 requirements influence population and community dynamics [7, 8]. This is surprising, given

49 the strong theoretical development of energetics as a fundamental determinant of
50 ecological processes such as reproduction, dispersal, and interactions with other organisms
51 [9]. For example, the Metabolic Theory of Ecology (MTE) has a long heritage of applying
52 universal scaling laws for the relationship between metabolic rate, body size, and
53 temperature (Box 1), to understand how energetics might govern ecological patterns [10-
54 14]. While MTE lends itself to interpretation of large scale macroecological or evolutionary
55 patterns [13, 15], there are well-recognised limitations to what MTE can tell us about the
56 variation in organismal responses to changing environmental conditions or management
57 regimes [8]. In essence, universal scaling laws focus on conformity to a generalised
58 relationship between metabolism and body size, rather than on inter- and intraspecific
59 variability around the central tendency. One might reasonably argue that MTE predictions
60 have little value in understanding why two similar-sized species, with similar metabolic
61 rates, can respond quite differently to human disturbance or environmental change [9]. For
62 ecologists and conservation biologists, then, there are important limitations on the
63 relevance and application of metabolic scaling laws to 'real-world' questions at the spatial
64 and temporal scales at which ecologists typically work.

65 The pressing challenge ahead lies in how to predict species responses to changing
66 environments, and how to quantify these responses in free-living organisms at scales that
67 are relevant to the interaction between the physiological traits of an organism and the
68 environmental constraints on ecosystem energetics. Recent advances in monitoring the
69 ecophysiological responses of free-living organisms might hold promise for greater
70 predictive understanding of species distribution patterns across a wider range of scales.
71 Unlike the traditional comparative physiology paradigm, which is primarily devoted to

72 quantifying the physiological responses of species under idealised conditions, 'ecological
73 energetics' aims to quantify the role of physiological processes in the ecological relations of
74 animals (and plants) in their natural habitats [8]. Ecologists, of course, have been quick to
75 point out that conditions are far from 'ideal' in the real world, and have been hesitant to
76 adopt comparative physiological approaches. In ecological energetics, by contrast, the
77 essential point is that any fundamental energetic traits determined by an organism's
78 physiology are only ecologically relevant in the context of environmental constraints
79 imposed on the availability or distribution of energetic resources [7-9, 16, 17]. For instance,
80 the movement of animals throughout the landscape is largely driven by the interaction
81 between a motivation to access resources (be they energetic, or reproductive), and the
82 energy required to access those resources by making movements across or around
83 physiologically-challenging environmental barriers [7]. To a great extent, then, the presence
84 and local abundance of a species in a landscape might be driven by the suitability of the
85 landscape for the animal's physiology.

86 In this article, we argue that the field of 'ecological energetics' is on the cusp of
87 transforming the mechanistic study of ecological dynamics within the context of changing
88 environmental conditions. We synthesize current understanding of the energetic basis to
89 ecological processes (Figure 1) and explore how the widespread application of ecological
90 energetics could provide a more mechanistic understanding of the complex interplay
91 between physiological constraints and environmental limitations. We then describe recent
92 advances in the technology required to cheaply and effectively test model predictions by
93 measuring metabolic rate (amongst other traits) in a wide range of free-living animals.
94 Finally, we provide empirical examples of the ways in which these principles can re-shape

95 our understanding of conservation management in changing ecosystems. The study of
96 energetic processes should no longer remain a specialised domain of physiology that
97 ecologists avoid [8]. Instead, fields as diverse as ecology, conservation biology, natural
98 resource management and landscape restoration will find important benefits in the
99 application of ecological energetics.

100

101 ***Ecological energetics: integrating physiological requirements within environmental***
102 ***constraints***

103 What we refer to as ‘ecological energetics’ represents the interpretation of
104 ecophysiological data on organismal energy dynamics within the broader template of
105 ecology and environmental management (Figure 1). Ecological energetics incorporates
106 physiological responses to the environment extending beyond trying to understand
107 fundamental energy requirements (such as thermal tolerance, thermoregulation and water
108 turnover; red pathways in Figure 1), to recognise that many aspects of individual
109 performance (the ‘realised ecological distribution’ in Figure 1) are constrained by the abiotic
110 environment and/or by ecological interactions with other organisms (such as ecosystem
111 productivity, competition, and associated costs of growth and reproduction; blue pathways
112 in Figure 1). The domain of ecological energetics, therefore, is where the physiological
113 requirements of organisms intersect the ecological constraints of the environment (the
114 green regions of overlap in Figure 1).

115 Our synthesis of the principles underpinning ecological energetics (Figure 1) is
116 founded on mechanistic, process-driven relationships between organisms and their
117 environment [18]. We see this as fundamentally different from a purely correlative

118 approach to measuring ecophysiological responses or species distribution modelling,
119 because it develops a niche envelope model incorporating the full range of physiological
120 tolerance limits, rather than those that are constrained by the ecosystems in which the
121 organism currently dwells. Of course, it is simply not practical to depict all of the potential
122 mechanistic pathways of energy flow in Figure 1, but the ultimate goal of ecological
123 energetics is to model these processes as precisely as possible, at spatio-temporal scales
124 that are relevant to a broad range of hypotheses. Process-based models have a greater
125 capacity than correlative models to predict beyond current ecological scenarios into novel
126 ecological space (and time), a key advantage when predicting the outcomes of rapid
127 environmental change, and articulating evidence-based management responses.

128 In ecological energetics, there is clear recognition that different environments impart
129 different challenges for organisms with different physiological traits (Figure 1). By the same
130 reasoning, it should be evident that management actions might need to prioritise different
131 aspects of ecophysiological requirements or ecosystem energetic limitations to achieve
132 diverse outcomes. For example, a successful single-species translocation program (Figure 1,
133 bottom left) might prioritise the suitability of habitat that falls within the species'
134 fundamental physiological tolerances (e.g. [19]), prior to quantifying potential ecosystem
135 energetic limitations or theoretical carrying capacities (e.g. [20]). By contrast, multi-species
136 ecosystem restoration (Figure 1, top left), might focus on identifying the diverse taxa that
137 can provide key ecosystem services (e.g. [21]), prior to identifying the fundamental
138 energetic requirements of the individual species. By quantifying the feedback loops detailed
139 in Figure 1, it should be possible to inform the real-world responses of organisms and
140 ecosystems to anthropogenic changes (both interventionist and unanticipated). Some of

141 these responses can best be quantified using 'classical' ecological approaches, but many can
142 be measured accurately only by incorporating an ecological energetic perspective.

143

144 *Generating process-based hypotheses*

145 To be of practical value, conceptual models such as those depicted in Figure 1 must
146 be translated into practical hypothesis-testing tools that can deliver evidence-based
147 outcomes. For example, the energetic responses of individuals to variation in climate are
148 likely to be important drivers of population-abundance patterns [22], yet Clarke [23] argued
149 strongly that a clear framework linking physiology, climate, and macroecology is still lacking
150 (but see [5]). Correlative models, though useful, can provide misleading predictions under
151 novel scenarios such as climate change [4, 5], and even some process-based models such as
152 MTE can be uninformative if applied at inappropriate scales (Box 1). Fortunately, significant
153 recent advances have also been made in the development of spatially-explicit niche
154 envelope models that provide increasingly powerful tools to make the connections between
155 physiological energetics, changing environmental conditions, and shifting patterns in the
156 distribution and abundance of organisms [5].

157 In process-based models, climatic parameters are used to predict local microclimatic
158 conditions, which can be integrated with known behavioural and thermal responses of the
159 focal species to solve energy-, mass- and momentum-balance calculations [24]. This
160 approach generates spatially-resolved predictions of microhabitats inhabitable by a focal
161 species, producing an estimation of its 'thermodynamic niche' [25]. This mechanistic
162 approach allows the prediction of distributional changes in response to novel environmental

163 change scenarios. While any given process-based model might incorporate only a few of the
164 many ecological and evolutionary feedbacks inherent in Figure 1, there is real heuristic
165 advantage in placing these within a broader, more holistic conceptual context. Such an
166 approach can be broadly applicable to a number of scenarios, including modelling habitat
167 use, the movement [26] or activity patterns [27] of animals, the distributions of rare or
168 range-restricted fauna (e.g. [19, 24, 28]), the energetics of migration [29, 30], the invasive
169 spread of non-native organisms [5], and predicted effects of climate change on phenology
170 [31], survival and reproduction [32]. Recent advances have seen mechanistic distribution-
171 models incorporated with energy budgets ([25, 33]; Box 1) to predict species' distributions
172 on the basis of ecological requirements for persistence and reproduction.

173 What might not be intuitively obvious about process-based models is in the process
174 of predicting 'habitable' ecological space, they effectively rule out vast sections of
175 hypothetical niche space as being metabolically inaccessible. For example, tolerance
176 thresholds and thermal response curves [34] can identify metabolically intolerable
177 ecological space where a species cannot survive or reproduce [5]. This in itself might provide
178 useful management guidelines for proposed translocation sites [32], or identify geographic
179 space that represents a barrier to the natural dispersal of animals through a landscape,
180 implicitly disrupting the ecological services that they provide (such as pollination or seed
181 dispersal). Quantifying the magnitude of these constraints informs the levels of
182 management required to ameliorate human impacts.

183

184 *A new generation of techniques for testing ecological energetic hypotheses*

185 It is important to point out that informative predictive models of species distribution and
186 abundance are not end-points in their own right, but are hypothetical starting points for
187 further empirical testing, particularly where they inform applied conservation outcomes. For
188 example, a model might predict climatically-suitable translocation sites for endangered
189 species [32], but local historical variation in land-use or productivity might impose energetic
190 constraints on the ability of a translocated population to survive and reproduce
191 (represented by the ecological feedbacks of Figure 1, *sensu* McNab [35]). The modelling
192 itself could prove futile if not interpreted in its full ecological context, and this highlights the
193 importance of field measurements of metabolic rate (and other physiological parameters) in
194 varying environments. Only now are the techniques for making these kinds of
195 measurements becoming readily available to ecologists in the field.

196 For ecologists, it has traditionally been difficult to extrapolate laboratory-based
197 measures of energy requirements, as simple multiples of the Basal or Standard Metabolic
198 Rate (BMR or SMR respectively [36-38]), to dynamic ecological scenarios. What is required
199 are measures of field metabolic rate (FMR) in free-ranging animals [39] that reflect the cost
200 of existence for that animal in its natural environment. A wide array of techniques are now
201 available to measure the energetic requirements of nearly all animal taxa in almost any
202 environment, centred around two intrinsic scaling approaches: the scaling of isotope
203 measurements (Box 2) or biotelemetry data (Box 3) with FMR.

204 In isotopic approaches, the differential elimination of hydrogen and oxygen isotopes
205 (doubly-labelled water; DLW) has been used as a measure of the water turnover rate and
206 FMR for more than 50 years (Box 2), but has not found widespread application outside

207 ecophysiology. It is only in recent years that strong evidence has emerged to support other,
208 more cost-effective and equally accurate approaches to measuring FMR across the breadth
209 of taxa, environments and temporal scales at which ecologists work. For example, the
210 biological elimination of radio-isotopic rubidium has been shown to scale reliably with FMR
211 in a wide range of organisms including very small taxa dispersing over large spatial scales,
212 such as insects [40], which have not previously been within the scope of reliable FMR
213 measurements (Box 2).

214 In a complementary set of approaches, the miniaturisation of electronics over the last
215 decade has allowed cheap and effective measurement of heart rate or body movement
216 using telemetry to calculate FMR at unprecedented spatial and temporal scales (Box 3). The
217 fundamental assumptions of the approach are that activity requires energy at a predictable
218 rate that scales from cellular metabolism, and that energy use can be calculated from the
219 provision of oxygen to the tissues by blood-flow from the heart.

220 Each technique has its own assumptions, costs and benefits (Table 1), presenting a
221 wealth of affordable and accurate avenues for ecologists to measure the physiology of an
222 organism in its 'natural' state. Despite this, the measurement of FMR and its subsequent
223 interpretation within energy budgets has rarely been extended to any applied ecological
224 investigation or management outcome [19, 32, 41-44]. With these technical advances, the
225 way is now clear to measure and interpret the physiological constraints on organisms at
226 spatio-temporal scales that were previously unachievable for ecologists and conservation
227 managers.

228

229 *Real-world applications of ecological energetics in conservation management*

230 In many respects, the 'adaptive management' paradigm of threatened species
231 conservation [45, 46] masks a failure to understand the mechanistic basis of threatening
232 processes or management actions (see [45] for examples). With an increased capacity to
233 predict and measure the energetic responses of organisms to varying environmental
234 conditions [22, 47], comes the ability to translate empirical measurements into practical,
235 real-world outcomes. Here, we present a series of contrasting examples of the schema
236 conceptualised by Figure 1, published and hypothetical, that show how ecological energetics
237 can be used to develop a more predictive understanding of conservation management
238 actions. Current ecological and management applications are typically single-species
239 focused, but already show evidence of how cascading effects across species interaction
240 networks might be modelled more effectively in an ecological energetics framework.

241 At the species level, mechanistic modelling (contextualising the red pathways in
242 Figure 1) has shown how extreme climate-warming could impact reproductive processes (in
243 this case via altered incubation temperatures and juvenile thermal tolerance; Figure 1) in
244 the endangered tuatara (*Sphenodon guntheri*) in New Zealand, leading to functional
245 extinction by the mid-2080s [32]. The model also predicted thermally-suitable translocation
246 sites for insurance populations in the face of climate change [32], but these predictions
247 were not empirically tested by monitoring real translocated populations, nor by applying
248 expectations of FMR to known ecological productivity to estimate carrying capacity (the
249 blue pathways in Figure 1). This type of mechanistic quantification of the effects of climate
250 change to provide clear management targets [24] is rare, but is emerging as a more
251 detailed, robust and powerful management tool for species of conservation significance [19,

252 20, 48]. However, there is still a requirement to incorporate empirical tests of predictions
253 under varying environmental contexts if any level of confidence is to be assigned to these
254 models.

255 In a contrasting example, the key threatening process for kittiwakes (*Rissa tridactyla*)
256 nesting in the Arctic Circle is human overfishing of food resources rather than climate
257 warming, imposing a different set of energetic limitations on population persistence. The
258 quantified energetic requirements of kittiwake foraging depend on time away from the nest
259 [49] and local food availability [50], with an upper physiological limit on flight time and
260 distance that the birds can cover [51]. Poor foraging success can reduce energetic reserves
261 and consequently reduce reproductive output. Overfishing greatly exacerbates natural
262 cycles of food availability, creating an ongoing reduction in foraging efficiency, with
263 substantial population-level implications for kittiwakes. In this case, the focal species
264 approach allows the estimation of cascading ecological feedbacks (blue pathways in Figure
265 1) between overfishing, reduced seabird foraging success, and energetic limitations,
266 potentially leading to reduced reproductive output and population decline. However, most
267 of these ecological feedbacks were not underpinned by mechanistic relationships *per se*,
268 thus reducing the predictive power of the model. In addition, there will be a need to better
269 consider variation in species' physiological tolerances (incorporating the red pathways in
270 Figure 1) when testing whether management actions, such as increased fisheries exclusion
271 zones around nesting habitats, might be particularly important in low productivity, rather
272 than high productivity, years [52]. Nevertheless, this example does highlight how even a
273 species-focused model can have community-wide relevance, because the driving
274 mechanisms operate through a cascading series of effects of overfishing on marine food-
275 webs, and ultimately influence the foraging and reproductive capacity of seabirds.

276 Detailed focal-species models have not yet been expanded to explicitly combine
277 quantitative energy budgets for multiple interacting species (Box 1). Notwithstanding, there
278 are no conceptual limits to applying ecological energetics to species interaction networks. In
279 practice, with current technology, there will be severe analytical constraints on the
280 modelling of energy budgets for even a modest number of interacting species. But even at
281 this level, explicit energetic modelling of simplified interaction networks could prove crucial
282 for predicting management outcomes. For example, Bergstrom *et al.* [53] describe the
283 unforeseen ecological outcomes of manipulating the complex predator-prey relationships of
284 feral cats and rabbits in the fragile sub-Antarctic ecosystem of Macquarie Island. The
285 management scheme compromised seabird populations when the biological control of
286 rabbits caused cats to seek alternative prey, and subsequently compromised native
287 vegetation when belated cat eradication released predation pressure on remaining rabbit
288 populations. Mechanistic models describing the realised ecological distributions of both cats
289 and rabbits (constructed from the red pathways and quantified using the blue pathways of
290 Figure 1) could have been used to model hypothetical scenarios, such as the effect of single-
291 species eradication (of either cats or rabbits) on the spatial dynamics of the other species.
292 For example, reducing the rabbit population would increase density-dependent competition
293 for food in cats, resulting in either prey-switching or predator population decline. The
294 potential impact could be quantitatively predicted by scaling the energetic value of
295 alternative prey items compared to rabbits to estimate the magnitude of predation rates on
296 alternative prey species (such as native seabirds). Similarly, the inspection of ecosystem
297 energetics and ecological feedback loops in Figure 1 would suggest that the effects of
298 subsequent cat eradication could be quantified by scaling the grazing rate of rabbits by the
299 energetic value of foraging and the rate of increase of rabbit populations under reduced

300 predation pressure. Although this is a hypothetical example, the potential advantages in
301 linking energetic models for multiple interacting species of management concern certainly
302 warrants empirical evaluation.

303 Exactly how far the community-wide, or even ecosystem-wide, application of
304 ecological energetics can effectively be developed remains to be seen. Notwithstanding the
305 many conceptual and methodological challenges yet to be overcome, we speculate that
306 ecological energetics will come to play an important role in many aspects of ecosystem
307 management. As an example, we consider how ecological energetics could play a crucial
308 role in ecosystem management through the ambitious global target of restoring 150 million
309 ha of degraded land by 2020 [54]. As pointed out by Menz and colleagues [54], successful
310 ecological restoration extends beyond the replacement of vegetation cover, to the recovery
311 of species interactions and ecological functioning [54, 55]. The mechanistic, process-based
312 approach underpinning ecological energetics could have great utility in the restitution of
313 biologically-mediated interactions between plants and mutualists [21, 56], where ecosystem
314 services (such as pollination or seed dispersal) might easily fail when the energetic
315 requirements of key vectors are not met in the restored ecosystem. Speculatively, we might
316 envisage a mechanistic model describing how changing land use patterns (such as clearing
317 and subsequent restoration efforts in a mining landscape) might alter the thermo-energetics
318 of key insect pollinators. The response of key taxa could not be accurately predicted using
319 correlative approaches because they would be operating in a novel ecological space. They
320 could, however, be predicted using niche envelope mapping and dynamic energy budgets,
321 informing novel approaches to restoration programs (such as seed mixes that promote
322 higher floral energy availability) to encourage the successful return of key pollination
323 vectors. The successful return of pollinators presumably has down-stream impacts through

324 better vegetative establishment, more rapid restoration success and increased biodiversity
325 leading to positive ecological and ecosystem energetic feedbacks (see Figure 1). These
326 hypothetical responses would have to be rigorously tested by measuring the
327 ecophysiological performance and population recruitment of key insect taxa under the
328 different management interventions hypothesised. However, we expect that understanding
329 and modelling the specific energetic requirements of key taxa will substantially increase the
330 cost-effectiveness of restoration and species translocation efforts.

331

332 *Conclusion*

333 The energetics of individual animals and the flow of energy through ecosystems
334 underlies many of the important processes that structure realised ecological niches,
335 community structure and ecosystem dynamics [7, 8]. Sagarin and colleagues [22] suggest
336 that the paucity of such information across the entire range of a species could be remedied
337 by the integration of new technologies and cross-disciplinary collaborative efforts. Although
338 techniques for quantifying energetics have existed for more than 50 years, advances in the
339 last few years now make the measurement of ecological energetics more accessible to field
340 ecologists than ever before, offering the opportunity to test hypotheses about the role of
341 energetics in ecology and evolution at a scale and level of detail that has previously been
342 impossible (*e.g.*[18, 33, 57]). Despite the importance of understanding ecological energetics,
343 recognition of the significance and accessibility of this information remains limited at the
344 applied level, and as such the ecological energetic component of most ecosystems or target
345 taxa remains a substantial knowledge gap in management programs [58]. We strongly
346 advocate the incorporation of ecological energetics into conservation management and
347 restoration plans at all scales and levels of application, from local to international. Given the

348 simplicity and low cost of emerging technologies, a broader application of ecological
 349 energetics offers one avenue to bring a more mechanistic, process-based foundation to
 350 science, management, and policy in an era of rapid environmental change.

351

352 **Acknowledgements**

353 This work was funded by an Australian Research Council Linkage grant LP110200304. SGA
 354 was supported by an Australian Post-graduate Industry Award under ARC Linkage grant
 355 LP0990428. RKD was supported by an ARC Future Fellowship FT100100040. We thank David
 356 Watson and Nick Isaac for constructive comments that greatly improved the manuscript.

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580 **Table 1.** Summary of recently-developed techniques for the measurement of field metabolic rate (FMR) in free-living organisms, with
 581 limitations and applications to the study of ecological energetics in a range of target taxa. DLW = doubly labelled water; ^{86}Rb k_b = radioactive
 582 rubidium turnover; HRT = heart rate telemetry; DA = dynamic accelerometry.

Technique	Limitations on organism size	Limitations on environmental application	Limitations on trophic level	Model taxa
Isotopic techniques				
DLW	Medium to large. The high metabolic rate and metabolic water production of small animals often means that complete isotope washout occurs very rapidly. Also, body fluid subsampling is logistically challenging in small animals.	Dry environments provide the most accurate DLW application because high water intake or water turnover relative to metabolic rate often result in overestimates of CO ₂ production. Fossorial environments result in re-enrichment and underestimates of CO ₂ production.	Liquid diets are problematic, as are diets with high incidental water intake (such as in fish) because they often lead to high water turnover and overestimates of CO ₂ production.	Reptiles, birds, mammals

Technique	Limitations on organism size	Limitations on environmental application	Limitations on trophic level	Model taxa
⁸⁶ Rb k _b	Small to medium. ⁸⁶ Rb persists for longer periods in small animals than DLW, reducing washout issues, and the whole body counting obviates the need to subsample body fluid. Large animals require larger doses of radiation to be effective, and this becomes a safety hazard.	All environments. Urban environments provide something of a legislative challenge, since enriched animals could present a public health risk and loss of enriched animals might technically constitute uncontrolled radioactive waste. It must be stressed that levels of enrichment are very low, and the risk is minimal.	Potassium rich diets are likely to result in higher ⁸⁶ Rb k _b and an overestimate of CO ₂ production. Thus, frugivores might be problematic for this technique.	Insects, amphibians, small birds, small mammals
Telemetry techniques				
HRT	Medium to large.	Open and uncluttered environments where telemetry signals are less likely	N/A	Birds, mammals,

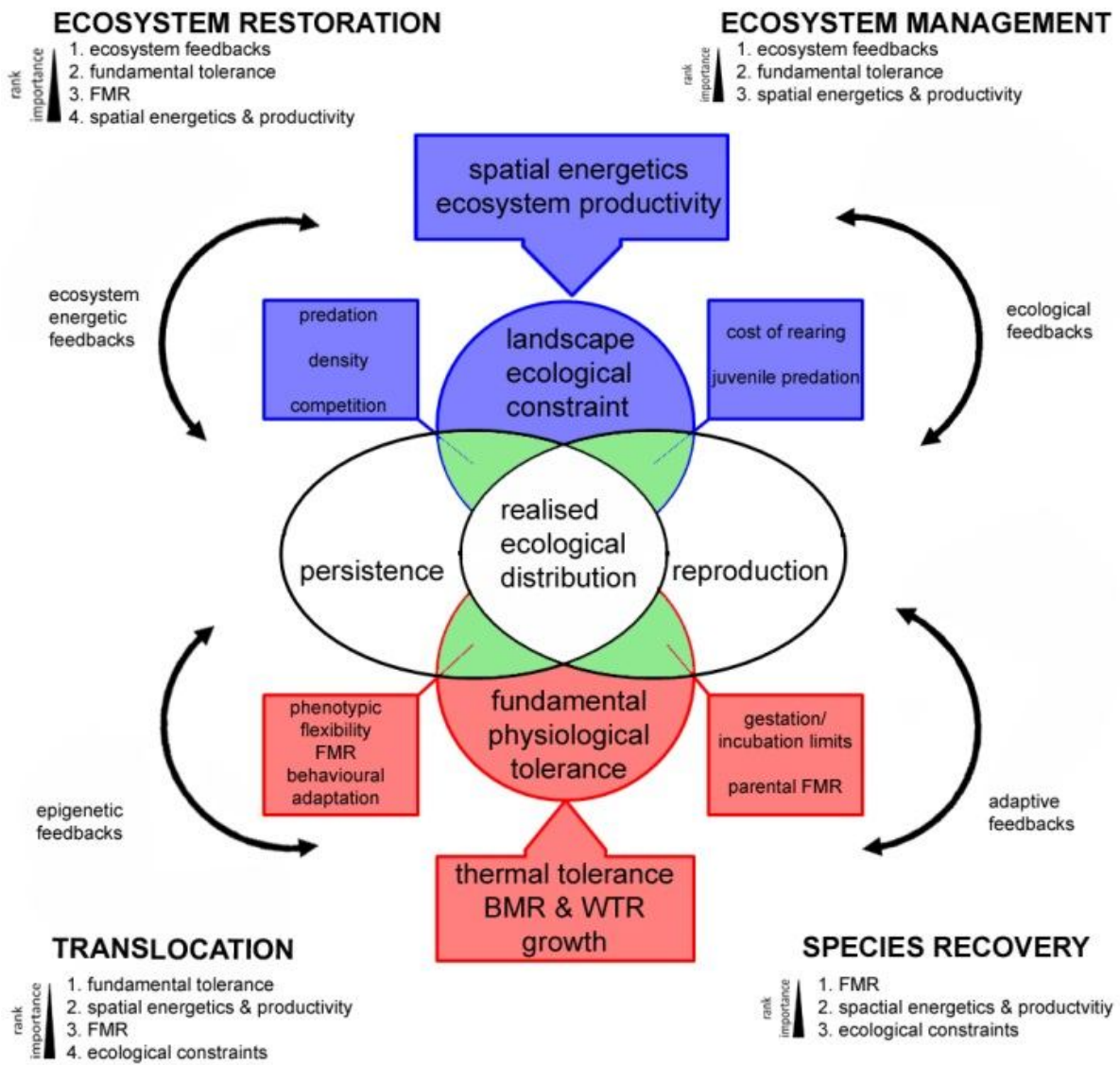
Technique	Limitations on organism size	Limitations on environmental application	Limitations on trophic level	Model taxa
	Body size is a factor of ethical consideration when instrumenting an animal. There is also a lower limit to what is technically possible, and small instruments are often associated with very short battery life.	to be scrambled by reflectance. Marine environments.		especially marine birds and mammals
DA	Medium to large. The lower limit to what is technically possible is smaller than HRT, but ethical considerations and very short battery life are important issues with small instruments in small animals.	All environments.	N/A	Birds, mammals, especially marine birds and mammals

584 **Figure caption**

585 **Figure 1.** Schematic illustration of the key pathways in the application of ecological
586 energetics to environmental management. For simplicity, not all potential pathways are
587 shown. Red pathways (bottom of diagram) represent animal energetic requirements,
588 established from mechanistic physiological data. Blue pathways (top of diagram) represent
589 landscape energetic limitations dictated by the biotic and abiotic environment. Green areas
590 indicate regions where ecological and physiological constraints interact to influence
591 ecological energetic requirements, and represent the domain of ecological energetic
592 studies. Black pathways indicate the ecological energetic feedbacks influencing ecosystem
593 stability. Differing management outcomes (such as ecosystem restoration, ecosystem
594 management, species recovery or translocation) will require a different rank ordering of
595 emphasis on different components of animal energetic requirements vs landscape energetic
596 limitations. See text for a detailed explanation.

597

598 **Figure 1**



599

600

601 Box 1. Energy as the currency of ecology

602 The budgetary interpretation of ecosystem dynamics holds that energy is the central
603 currency of ecology [59]. Ecological energetics aims to understand potential energetic
604 constraints imposed on ecological patterns and processes by the metabolic requirements of
605 interacting organisms. The metabolic basis to ecological energetics forms the foundation for
606 a diverse set of mechanistic approaches to modelling species distributions, from expansive
607 cross-species models such as the Metabolic Theory of Ecology (MTE), to intensive within-
608 species models such as Dynamic Energy Budgets (DEBs) [10, 14].

609 MTE proposes that a universal scaling law defines the relationship between body
610 size, metabolic rate and temperature, and can predict ecological patterns at the population-
611 [9], community- [9], or even ecosystem level [13, 15, 16]. The strength of this approach is
612 that MTE can generate broad-scale macroecological predictions from a minimal number of
613 parameters, which match some observed ecological patterns with remarkable accuracy [15,
614 60]. However, contentious debate surrounds the theoretical basis of MTE's power law
615 exponent [11, 61], and the empirical fit to field data [10, 13]. There is also the broader
616 criticism that MTE inherently focuses on cross-species scaling trends, and brings little
617 mechanistic understanding to the (frequently large) degree of variation around the scaling
618 relationship [10, 12, 62], particularly in terms of metabolic and physiological responses to
619 varying environmental conditions [63]. Moreover, MTE might be considered 'naïve' to the
620 flexibility and complexity of the interplay between ecological and evolutionary processes
621 (Figure 1) that shape species responses and adaptation to changing environments.

622 Single-species DEB models counter many of the inherent limitations of MTE for
623 predicting species responses to environmental variation, by solving physiological

624 maintenance and structural growth equations for focal organisms [64, 65]. DEBs provide a
625 comprehensive underpinning to species-specific energetic constraints, which have recently
626 been incorporated into species distribution models [18, 33], predicting distribution on the
627 basis of ecological requirements for persistence and reproduction. A DEB delivers a flexible
628 model of energetics that can be applied in ecological space to estimate distribution and
629 abundance resulting from changing physiological or energetic demands of the landscape,
630 rather than relying on generalised macroecological scaling rules.

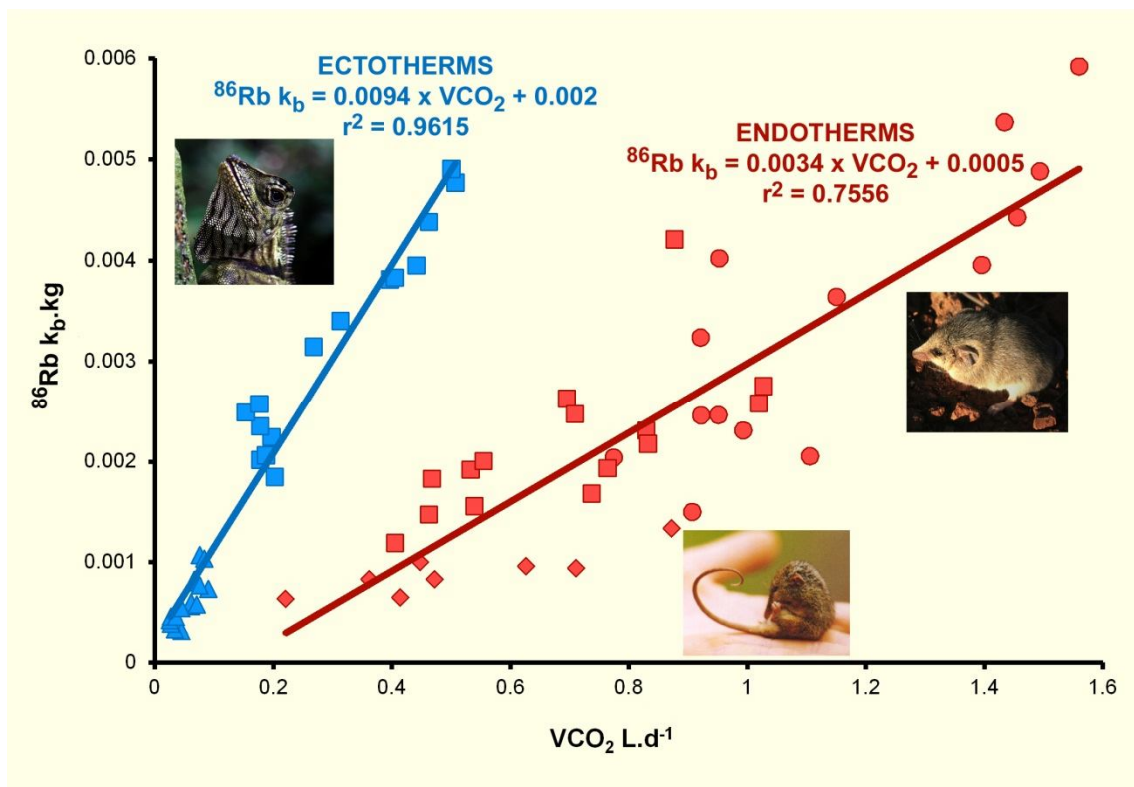
631 A future challenge is how to capitalise on the predictive power of DEBs at the spatial
632 and temporal scales that are most relevant to conservation management. Moreover, the
633 ability to predict the cascading community-wide effects of environmental change by
634 integrating DEBs for multiple interacting organisms remains unresolved.

635 Box 2. Advances in isotopic techniques for measuring field metabolic rate

636 The application of comparative physiological methods to free-living organisms in their
637 natural environment has always been the 'holy grail' of ecophysiological studies. The
638 measurement of Field Metabolic Rate (FMR) and Water Turnover Rate (WTR) in free-ranging
639 animals began with the work of Lifson and McClintock [66] and led to the development of
640 the doubly-labelled water (DLW) method to directly measure energy expenditure and water
641 flux in wild animals [67]. The rationale is that heavy isotopes of oxygen (^{18}O) are lost from an
642 organism as both CO_2 and H_2O , whereas heavy isotopes of hydrogen (^2H or ^3H) are lost only
643 as H_2O [68, 69]. Therefore, the difference between the hydrogen and oxygen isotope
644 turnover rate is indicative of CO_2 production [68, 69], which is linked to metabolic rate and
645 energetic requirements. However, there are several assumptions behind the DLW technique
646 that are not always met [67, 68] (see Table 1), thus restricting its use in some taxa, such as
647 amphibians [70], diving birds or mammals [71], and organisms of small body size [72-74].
648 Finally, the ^{18}O isotope is expensive to procure and analyse [68, 69], and these costs have
649 proven prohibitive for widespread general application in ecological studies [68].

650 Alternative techniques to measure FMR have long been sought to overcome the
651 constraints of DLW, including administering doses of various radioactive isotopes to
652 determine whether radio-isotope elimination rate scales with metabolic rate [75]. Several
653 isotopes have been investigated in this regard [76-79], and rubidium (^{86}Rb) has been found
654 to have the highest correlation with metabolic rate [73, 74, 78, 79]. Practically, the isotope is
655 introduced by ingestion or intraperitoneal injection [73, 74] similar to the stable isotopes
656 used in the DLW technique. The subsequent rate of elimination (termed biological turnover;
657 k_b) is proportional to the rate of CO_2 production ($\text{LCO}_2\cdot\text{d}^{-1}$). Measuring ^{86}Rb turnover reduces

658 body size limitations and increases the temporal measurement period [73], as well as
 659 providing the capacity to measure the FMR of very small animals, including invertebrates
 660 [74], much more accurately than DLW. However, as yet there is still a paucity of validation
 661 data comparing ^{86}Rb turnovers to CO_2 production across a wide range of organisms [73, 74].
 662 One of the challenges to be considered in the use of radioisotopes is the justifiable public
 663 resistance to potential contamination. In general, the regulatory guidelines concerning
 664 environmental and public health concerns can be easily adhered to without risk to data
 665 integrity.



666

667 **Box 2, Figure I.** A meta-analysis of the relationship between rubidium isotope turnover and
 668 CO_2 production shows strong taxon-dependent scaling relationships [74]. All contributory
 669 regressions were significant, and differences between endotherms and ectotherms are
 670 speculated to relate to metabolic efficiency, unlike the expected isometry of DLW scaling
 671 relationships. See Tomlinson *et al.* [74] for further details of symbols and species surveyed.

672 Box 3. Biotelemetry as an alternative for estimating field metabolic rate

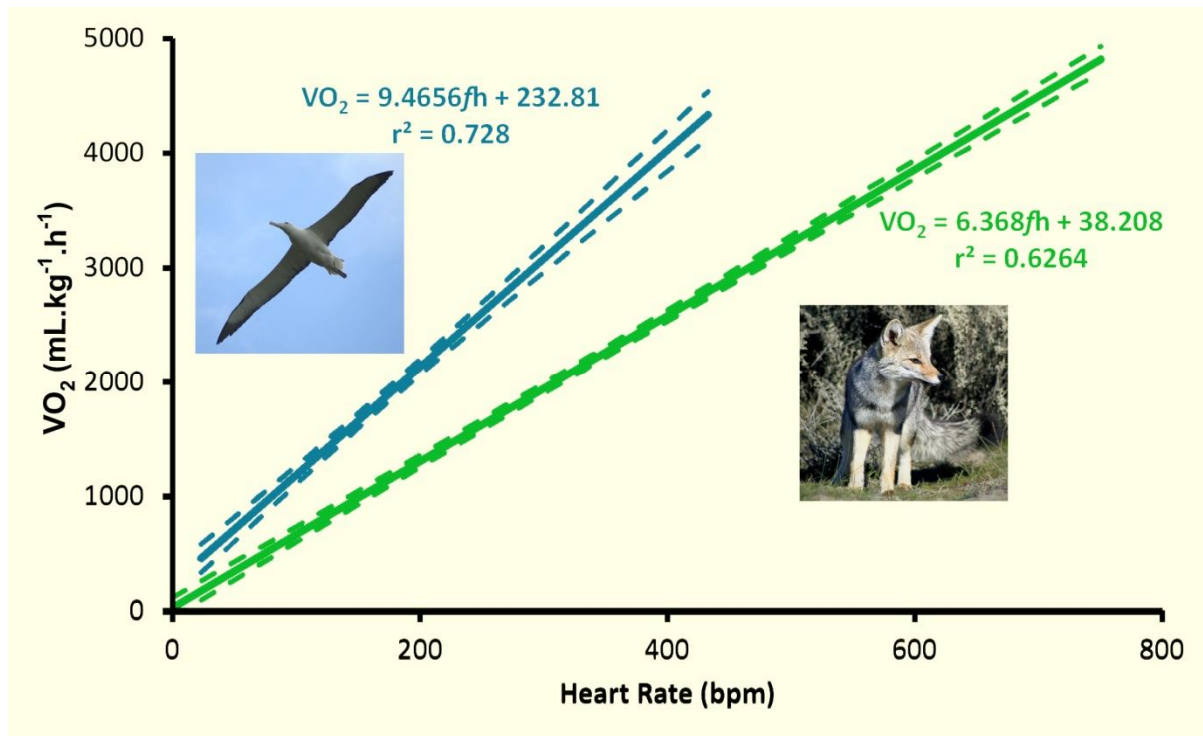
673 The most widely used alternative approach to isotopic scaling of FMR is telemetry
674 techniques that exploit the correlation between heart rate and metabolic rate (see [80] and
675 [81] for review). Theoretically, an increase in cardiac output is required to furnish increased
676 aerobic metabolism, including both physical activity and increased thermoregulatory
677 requirements [81]. Biotelemetry, such as Heart Rate Telemetry (HRT), involves
678 instrumenting the animal with a radio-telemeter or data logger in close enough association
679 to the heart or a major blood vessel to record individual heart beats. The HRT technique can
680 be implemented in a minimally-invasive manner, especially if the instruments are fitted
681 externally rather than implanted [82], reducing animal welfare concerns particularly in the
682 case of species of conservation significance. Butler and colleagues [83] discuss extensively
683 some other advantages of HRT, such as the ability to estimate the metabolic costs of specific
684 activities, and “value-adding” when other physiological or behavioural variables such as
685 body temperature, dive depth, acceleration and body position (attitude) are monitored
686 concurrently and correlated with other features of the animal's behaviour and environment.
687 A meta-analysis of studies that have measured heart rate and metabolic rate suggests that
688 metabolic rate scales predictably with heart rate (Box 3 Figure 1), but there remain
689 reservations concerning the accuracy of biotelemetry, because heart rate is only one of a
690 suite of physiological variables that drive changes in metabolic rate [80,81].

691 In contrast, dynamic accelerometry (DA) outfits the animal with a data logger that
692 measures movement (acceleration). The rationale is that animal movement requires the use
693 of energy, and that any movement should produce a corresponding, albeit dampened,

694 movement of the animal's trunk (or body core [84,85]). The DA technique is in its infancy,
695 and reservations remain over its accuracy [80, 86].

696 Unlike isotope techniques, neither biotelemetry approach has any constraints on the
697 period during which the animal has to be recaptured, because data can be logged and
698 stored, and the 'signal' does not degrade or become washed out over time [83]. However,
699 where telemeters are sufficiently small to measure heart rate or movement in small
700 vertebrates, the battery life of small units is very short [80], leading to potential
701 compromises on data quality. While there are some definite advantages to pursuing
702 biotelemetry technology, these techniques remain at the very edge of our technical
703 advancement, and need to be carefully considered with the help of a skilled practitioner.

704



706 **Box 3, Figure I.** A meta-analysis of the relationship between heart rate and oxygen
 707 consumption shows strong taxon-dependent scaling relationships in endotherms [82, 87-
 708 100]. Both regressions are statistically significant, with dashed lines representing 95%
 709 confidence limits. Data points have been omitted for clarity. Body masses of the species
 710 included range from 0.37 – 9.0 kg for birds, and 0.17 – 544.0 kg for mammals.

711 **Glossary**

712 *Basal metabolic rate (BMR)*: metabolic energy transformation in an organism in a rested,
713 awake condition, fasted for sufficiently long to be in a post-absorptive state, and in a
714 thermal environment that imparts no thermoregulatory requirement (the
715 thermoneutral zone).

716 *Biotelemetry*: the application of an automated communications process to collect data
717 remotely by monitoring various vital signs of an organism and logging or transmitting
718 the resulting data to receiving equipment. Although any physiological data could
719 theoretically be gathered, heart rate and movement patterns are often used to infer
720 FMR.

721 *Doubly-labelled Water (DLW)*: water in which both the hydrogen and the oxygen have been
722 replaced with heavy isotopes, forming deuterium oxide-18 ($D_2^{18}O$), differential
723 turnovers of which can be used to calculate FMR.

724 *Dynamic Energy Budget (DEB)*: theory that aims to identify simple quantitative rules for the
725 organization of metabolism of individual organisms that can be understood from basic
726 first principles. The theory integrates stoichiometric biochemical aspects of mass,
727 energy, time, surface area and volume. The word "dynamic" refers to the life cycle
728 perspective of the theory, where the budget changes dynamically over time.

729 *Ecological Energetics*: The integration of the physiological limits of an organism with the
730 ecological constraints (biotic and abiotic) of the environment where it lives. These can
731 be modelled mechanistically to generate hypothetical management guidelines, and

732 can be tested empirically by measuring the physiology of free-ranging organisms
733 within the environment.

734 *Energetics*: The branch of comparative physiology concerned with quantifying the metabolic
735 cost of various aspects of an organisms' biological activity, including BMR or SMR,
736 thermoregulation, digestion, growth, locomotion, reproduction, or any other set of
737 activities.

738 *Energy budget*: the sum total of metabolic transformation costs available to an organism
739 with which it might meet the requirements of normal biological activity.

740 *Field metabolic rate (FMR)*: the energetic requirement of an organism pursuing normal
741 biological activity, unrestrained in a natural environment, incorporating costs of
742 locomotion, thermoregulation, digestion and behavioural activities.

743 *Metabolic Theory of Ecology (MTE)*: an extension of Kleiber's Law which posits that the
744 metabolic rate of organisms is the fundamental biological rate that governs most
745 observed patterns in ecology. MTE is based on an interpretation of the relationships
746 between body size, body temperature, and metabolic rate across all organisms.

747 *Niche Envelope Mapping*: process-driven (mechanistic) species distribution modelling aiming
748 to link data on the limiting behavioural, morphological and physiological traits of
749 organisms in relation to changing climate and ecology. This approach is distinct from
750 correlative distributional modelling approaches, which inherently lack or have limited
751 predictive capacity.

752 *Rubidium-86 turnover* ($^{86}\text{Rb } k_b$): the biological elimination rate of radioactive rubidium, a
753 biological analogue of potassium, which scales with metabolic rate and can be used to
754 infer FMR.

755 *Standard metabolic rate (SMR)*: metabolic energy transformation in an organism under
756 specified standard conditions (often those defining BMR), or imparting specific
757 thermoregulatory requirements (i.e. thermal response curves)

758

759 **Outstanding Questions**

- 760 1. How can the influence of unpredictable shifts in spatial or temporal variability of
761 energetic resources be modelled effectively?
- 762 2. How can species that are not in ecological or evolutionary stasis be effectively
763 modelled with respect to changing patterns of distribution and abundance?
- 764 3. How well can epigenetic and memetic effects be incorporated into mechanistic
765 models of distribution and abundance, and how can these effects be tested using
766 ecological energetic approaches?
- 767 4. What are the inter-generational effects of changing ecological energetic constraints,
768 and how can these effects be predicted under scenarios of ongoing, rapid and
769 unpredictable change?
- 770 5. How do we manage ecological energetic factors crucial to human well-being where
771 they might be in conflict with energetic factors crucial to biodiversity and ecosystem
772 function?