




The ephemeral resource patch concept

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ABSTRACT

Ephemeral resource patches (ERPs) – short lived resources including dung, carrion, temporary pools, rotting vegetation, decaying wood, and fungi – are found throughout every ecosystem. Their short-lived dynamics greatly enhance ecosystem heterogeneity and have shaped the evolutionary trajectories of a wide range of organisms – from bacteria to insects and amphibians. Despite this, there has been no attempt to distinguish ERPs clearly from other resource types, to identify their shared spatiotemporal characteristics, or to articulate their broad ecological and evolutionary influences on biotic communities. Here, we define ERPs as any distinct consumable resources which (i) are homogeneous (genetically, chemically, or structurally) relative to the surrounding matrix, (ii) host a discrete multitrophic community consisting of species that cannot replicate solely in any of the surrounding matrix, and (iii) cannot maintain a balance between depletion and renewal, which in turn, prevents multiple generations of consumers/users or reaching a community equilibrium. We outline the wide range of ERPs that fit these criteria, propose 12 spatiotemporal characteristics along which ERPs can vary, and synthesise a large body of literature that relates ERP dynamics to ecological and evolutionary theory. We draw this knowledge together and present a new unifying conceptual framework that incorporates how ERPs have shaped the adaptive trajectories of organisms, the structure of ecosystems, and how they can be integrated into biodiversity management and conservation. Future research should focus on how inter- and intra-resource variation occurs in nature – with a particular focus on resource × environment × genotype interactions. This will likely reveal novel adaptive strategies, aid the development of new eco-evolutionary theory, and greatly improve our understanding of the form and function of organisms and ecosystems.

Key words: ecology, evolution, ecosystems, biotic communities, ecological theory, landscape heterogeneity, patch dynamics.

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I. INTRODUCTION

Resources are the fundamental template for biology, and their spatiotemporal patterning underpins every biological process – from shaping the fitness landscapes and evolutionary trajectories of species (Nyman, 2010; Robinson & Beckerman, 2013; Braga *et al.*, 2018; Sant *et al.*, 2021) to the structuring, patterning and movement of entire biological communities (Elton, 1949; Holling, 1992; Levin, 1992; Wu & Loucks, 1995; Aikens *et al.*, 2020; Abrahms *et al.*, 2021). There are many resource types, ranging from utility resources for predator avoidance and mating (e.g. tree hollows, mountaintops, and reproductive partners), to inorganic energy resources (e.g. sunlight, nitrogen, phosphates, water), to consumable organic resources for growth and development (e.g. plant tissue, carrion, plankton, and fungi) (Dennis, Shreeve & Van Dyck, 2006). The enormous variation among resources is what shapes organisms, creates heterogeneity in species distributions, and forms the structure and function of ecosystems. Understanding the spatiotemporal variability of resources is therefore central to a comprehensive synthesis of ecology and evolution.

One of the primary ways resources vary is in their longevity – from perennial resources like trees and rivers, which may persist for thousands of years, to ephemeral resources such as animal dung, carcasses, decaying plant matter, and temporary pools, which may only last hours or days (Fig. 1). These ephemeral resource patches (ERPs) are particularly interesting, as their finite and stochastic dynamics contribute greatly to the heterogeneity of landscapes (Hyndes *et al.*, 2022), amplify source–sink dynamics (Amarasekare & Nisbet, 2001), intensify resource competition (Rohlf & Hoffmeister, 2004), promote coexistence (Ives, 1991; Germain *et al.*, 2021), and greatly enhance biodiversity. Due to these unique dynamics, ERPs have long interested ecologists (Table 1) and have prompted the development of many central concepts from metapopulation dynamics to coexistence theory (Shorrocks, Atkinson & Charlesworth, 1979; Hanski, 1987, 1998; Finn, 2001).

Beyond ecology, ERPs have also shaped evolutionary processes at both local and metapopulation scales (Amarasekare & Nisbet, 2001; Altermatt & Ebert, 2010; Eldakar *et al.*, 2010) – from life histories (Sevenster & van

Alphen, 1993) to adaptive trajectories (Blanckenhorn, 1998; Bonduriansky, 2007), and genetic architectures (Mérot *et al.*, 2020). Because ERPs are so inherently variable, no two resources will exert the same selective pressures on their consumers (Lacy, 1984), and selection will also differ substantially among seasons and environments (Butlin & Day, 1989). This stochasticity means that for ERP consumers, optimal evolutionary strategies (e.g. adaptive tracking, phenotypic plasticity, bet hedging, dispersal syndromes) will fluctuate among resource types, environments, and over seasonal timescales (Simons, 2011; Armstrong *et al.*, 2016) – raising questions related to a wide range of evolutionary processes. For example: how does the extreme variability of ERPs shape dispersal syndromes, do optimal adaptive strategies change throughout seasons, and why are not all ERP consumers strongly dispersing, bet-hedging, generalists?

ERPs have also played much broader roles in shaping entire clades of the tree of life, including fostering the diversification of dung beetles (Gunter *et al.*, 2016), saprophagous flies (Yan *et al.*, 2020; Bayless *et al.*, 2021), parasitoid wasps (McLeish, Van Noort & Tolley, 2010), and puddle-breeding amphibians (Zimkus, Rödel & Hillers, 2010). These taxa all exhibit complex life cycles, where larvae experience selection in (often ephemeral) patches, whereas adults occupy broader landscapes. This adaptive decoupling between life stages has likely played a key role in the success of ERP consumers (Truman & Riddiford, 1999; Erezylmaz, 2006; Sherratt *et al.*, 2017; Collet & Fellous, 2019; Ten Brink, de Roos & Dieckmann, 2019). Nevertheless, the potent evolutionary forces stemming from ERPs have received scant attention, and it remains unclear how they have shaped many aspects of biological diversification.

A major reason for this is that while we can clearly appreciate the shared eco-evolutionary forces that ERPs exert on species, our actual definition of ERP remains conceptually vague. We know little about which spatiotemporal properties characterise ERPs, which resources share these spatiotemporal properties, or how these properties differ among resources and environmental contexts. Without such a framework, we cannot properly articulate or quantify the eco-evolutionary contributions of ERPs to organisms and ecosystems. Given the critical importance of ERPs in generating ecosystem heterogeneity (Finn, 2001; Barton *et al.*, 2019), maintaining biodiversity



Fig. 1. Examples of ephemeral resource patches. From left to right: a male *Tapeigaster* sp. (Diptera: Heleomyzidae) guarding a fungal sporocarp (the female oviposition site) from conspecific male competitors (credit: Nathan Butterworth). *Litoria citropa* (Anura: Pelodyadidae) amplexing in an ephemeral stream (credit: Ian Bool). Frit flies (Diptera: Chloropidae) feeding on bird dung (credit: Matt Bertone). Ants (Hymenoptera: Formicidae) foraging the micro-carcass of *Apis mellifera* (Hymenoptera: Apidae) (credit: Nathan Butterworth). *Milesia virginiensis* (Diptera: Syrphidae) ovipositing on decaying leaf litter (credit: Matt Bertone). *Chrysomya* blowflies (Diptera: Calliphoridae) at a possum carcass (credit: Nathan Butterworth). A goldenrod gall formed by *Eurosta solidaginis* (Diptera: Tephritidae) (credit: Matt Bertone). A cluster of seaweed flies (Diptera: Coelopidae) in marine intertidal wrack (credit: Nathan Butterworth).

(Benbow *et al.*, 2019; Maurice *et al.*, 2021), and shaping the evolutionary landscape (Van Tienderen, 1991; Blanckenhorn, 1998; Mérot *et al.*, 2020), we suggest that there is a pressing

need to define their parameters, their variability, and how they drive ecological patterns and evolutionary processes. This will unify the theory regarding these resources and their

Table 1. A history of the terminology relating to the ephemeral resource patch (ERP) concept. We have included terms that incorporate at least one type of ERP as defined by Beaver (1977). We also include the first recorded use of the term ‘ephemeral resource patch’ (Finn, 2001) as well as where, to our knowledge, the terms ‘ephemeral resource’ and ‘ephemeral patch’ first emerged in the literature [Shorrocks *et al.* (1979) and Doube (1987), respectively].

Term	Definition	Resources	References
Minor habitat	Centres of action in which interspersions between populations tends to be complete and ecological dynamic relations (at any rate among invertebrates) at their strongest. Although they may be so close and homogeneous (as for a <i>Phragmites</i> swamp or a crop plant) as to lose the qualities of obvious patterning, usually they are spaced out and repeated in the same form, partly regularly and partly irregularly.	Individual plants, decaying plants, nests, dung, carrion, decaying wood, tree-holes full of water, <i>Phragmites</i> swamps	Elton (1949)
General system	Small but rather concentrated and specialised centres of action formed not only by individual living plants like trees, but also by various kinds of dead matter, either in a state of decay or else artefacts of animals or man. These may occur scattered through the four major systems (terrestrial, aquatic, terrestrial–aquatic and domestic), as well as to a lesser extent in subterranean habitats.	Dying and dead wood, macrofungi, dung, carrion, animal artefacts (nests), human artefacts (crops, fenceposts).	Elton & Miller (1954)
Temporary habitat	The terms temporary and permanent are imprecise and relative. It is, however, easy to recognise the extremes: a dung pat lasts only a short while, allowing one or two generations to be passed in that location, whilst a large river may remain unchanged in its position for thousands of years and countless generations can live in the same location as their forebears. Such (temporary) habitats, being early stages in the biological succession, are only in one locality for a relatively short time. Some ponds are of a very temporary nature, soon drying out, others, notably the bog pools of heathlands and brackish ponds of saltings, are more permanent.	Dung, carrion, fungi, plant debris (e.g. logs, straw, hot-beds), and annual and perennial plants of seral communities (e.g. wastelands, fields)	Southwood (1962)
Non-equilibrium island communities	Small and distinct resources that consist largely of decaying organic matter. They form discrete habitat units or ecological ‘islands’ scattered through other habitats. These ecological islands are not self-sustaining, and the communities in them can never reach an equilibrium at least on the scale of the individual ‘island’. They consist of a limited amount of energy, which is gradually used up by the activities of the community members. The successional changes occur on a scale of days (or even hours) rather than years. Changes are largely the result of the activities of the organisms themselves. The physical environment often has relatively little direct effect. Because of the rapidity of the successional changes, there is usually only a single generation of any species (excluding microorganisms) before the habitat unit has become either unsuitable or exhausted. Dispersal is then necessary to find other suitable units for colonisation.	Dying or dead wood, dung, fungi, and animal carrion	Beaver (1977)

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Table 1. (Cont.)

Term	Definition	Resources	References
Ephemeral resource patch	Spatially and temporally delimited patches of high-quality resources. Typically, there is a limited period during which the patch is colonised, generally no more than one generation usually develops in each patch and the community composition of individual patches may be highly dependent on stochastic factors (Finn, 2001).	Leaf packs in streams, fruits, dung pads, mushrooms, carrion	Shorrocks <i>et al.</i> (1979); Doube (1987); Finn (2001)
Meroceneses	Scattered, small, and ephemeral microhabitats that are unstable.	Decayed wood, ant hills, bird nests, intermittent wetlands and streams, mammal nests	Napierała & Błoszyk (2013)
Necromass	Dead organic matter of either heterotrophic or autotrophic origin.	Decaying plant matter, animal carrion and dung	Benbow <i>et al.</i> (2019)

communities, generate new eco-evolutionary predictions, and allow us to incorporate ERPs better into the conservation of organisms and management of ecosystems.

In this review, we provide a refined definition of ERPs, outline their shared spatiotemporal characteristics, and place these into patch-scale and landscape-scale contexts. We then identify the key eco-evolutionary theory that underpins all ERPs and present a new unifying framework. Finally, we outline the utility of this framework by showing the implications of a general ERP concept for understanding evolutionary processes, ecosystem dynamics, and biological conservation.

II. DEFINING EPHEMERAL RESOURCE PATCHES

There is a need to define ERPs clearly so that we can articulate their shared spatiotemporal properties and begin to understand and quantify how these properties have shaped the eco-evolutionary trajectories of their consumers.

The primary characteristic of ERPs suggested by Beaver (1977) relates to their temporal dynamics – specifically, that the finite nature of an ‘ephemeral resource’ should preclude the survival of multiple generations and prevent a community equilibrium from being formed at the patch scale. Various resources have been referred to as ‘ephemeral’ – from small discrete patches of carrion to animal nests, intermittent streams, and entire habitats such as ephemeral wetlands (O’Neill, 2016). Yet only a subset of these meet Beaver’s definition of ERPs. For example, while landscape-scale ephemeral habitats such as wetlands are technically ‘short-lived’, they can support multiple generations of the same plant communities, as well as the same animal communities due to aestivation (Dietz-Brantley *et al.*, 2002; O’Neill, Rogers & Thorp, 2016). As a result, the community of a wetland patch at any given hydroperiod will be partially determined by the community of the preceding hydroperiod, potentially giving way to the establishment of a community equilibrium within the ephemeral wetland ‘patch’. This capacity to support

multiple generations of the same community due to predictable spatiotemporal characteristics also extends to many smaller aquatic habitats such as ephemeral ponds, rock pools, pitchers, and tree holes. These resources will often support multiple generations because they recur in the same location over time due to predictable hydro-regimes, particularly in the wetter seasons (Sota, Mogi & Hayamizu, 1994; Vanschoenwinkel *et al.*, 2009). While much of the theory we outline below will still apply to these resources, they are excluded as ‘true’ ERPs by Beaver’s (1977) original definition. We discuss these intermediate examples in more detail later in this section (see Fig. 2).

We must also consider the spatial properties of ERPs, which are varied and complex within a patch dynamics concept. The most basic definition of a patch is ‘a relatively homogeneous area differing from the surrounding matrix’ (Forman, 1995, p. 43) – which depends largely on both the spatial and temporal scales relevant to the focal organism(s) and the question being asked (Pringle *et al.*, 1988). However, there is a valid distinction to be made between patches in the context of entire habitats, and patches in the context of individual, discrete consumable resources. By distinguishing these scales, an ephemeral wetland is best considered an ephemeral ‘habitat patch’ composed of its own heterogeneous mixture of discrete consumable ‘resource patches’. Although this problem of scale could also be extended, for example, to an animal carcass comprising different tissue types (e.g. bone/fat/muscle) – where each tissue type is its own ‘patch’ – this narrowed view would fail to consider the relative homogeneity of the entire carcass compared to the heterogeneity of its surrounding environment. An exclusive consideration of fine-scale within-carcass tissue types as ERPs would also neglect any obligate consumers that feed broadly on the carrion resource patch and would overlook the interkingdom interactions (e.g. those between microbes, invertebrates, and vertebrates) that connect the ecological dynamics of the entire ‘resource patch’. We argue that any definition of a patch must consider not only the relative structural, chemical, and genetic homogeneity of the resource relative to its environment, but also the composition of its multitrophic

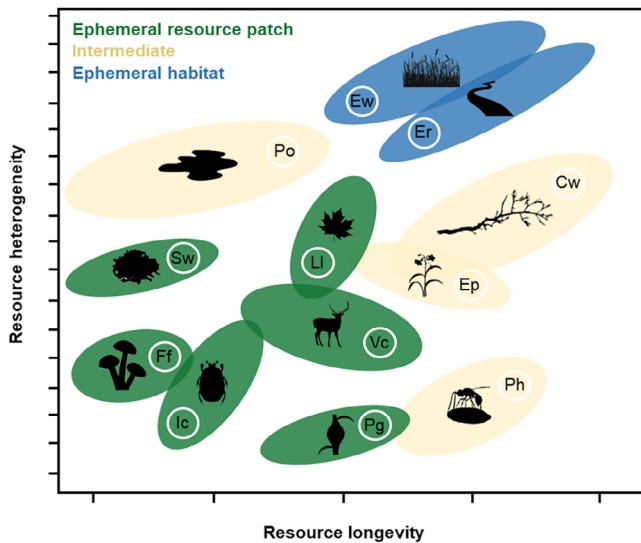


Fig. 2. Hypothetical variation in the longevity and heterogeneity of various ‘short-lived’ resources, highlighting the subtle distinctions between ERPs, intermediate examples, and ephemeral habitats. Ellipses represent hypothetical confidence intervals for each resource characteristic. Intermediate resources will contain some resources that fit within our ERP concept (i.e. short-lived parasite hosts) and others that do not (i.e. long-lived parasite hosts that support multiple generations of consumers). We define resource longevity as the average number of community generations for a given resource type. We define resource heterogeneity as the relative chemical, genetic, and structural homogeneity of the resource relative to its surrounding environment(s). These factors could be experimentally derived for a group of resources (for example, ephemeral pools) through empirical measurements of the longevity, chemical heterogeneity, and community dynamics of various pool types from different habitats. Abbreviations: Cw, coarse woody debris; Ep, ephemeral plant; Er, ephemeral river; Ew, ephemeral wetland; Ff, fungal fruiting body; Ic, invertebrate carrion; Ll, leaf litter; Pg, parasitic gall; Ph, parasitic host; Po, ephemeral pool; Sw, seaweed wrack; Vc, vertebrate carrion.

community. This is important because the characteristics of a ‘patch’ are not solely dependent upon the properties of the resource (e.g. chemical composition, size), but also on the properties of individual micro- and macro-consumers (e.g. feeding rates, metabolisms, sizes), and the interactions between these consumers (e.g. predation, mutualism, parasitism).

The challenge to defining the spatial extents of ERPs, therefore, is differentiating between intra-patch variability and patch matrix variability. We suggest the most pragmatic ERP concept is one that considers the ERP as the lowest level of patch homogeneity and community organisation that still facilitates consideration of the entire ‘patch’ community – that is, all consumers of the ERP as well as the inter-kingdom interactions occurring within the ERP [e.g. between gall midges and their mutualistic fungi (Rohfritsch, 2008; Kolesik

et al., 2019)]. Under such a concept, the gradients of nutrients/tissue types and associated microbial communities within an ERP would be considered as discrete ‘micro-patches’ within an ERP, and landscape-level ephemeral resources (such as an entire ephemeral wetland) would be considered as heterogeneous ephemeral ‘habitat patches’ interspersed within a mosaic of ERPs and other resource patches. Importantly, many of the ERP dynamics we outline below may still apply at this conceptual level (O’Neill *et al.*, 2016).

We therefore put forward a definition of ERPs that builds on earlier related concepts and identifies their common elements at the lowest level of patch and community organisation; one that accounts for obligate consumers and inter-kingdom interactions (Table 2). To meet our definition of an ERP, the following criteria must be met: (i) any distinct consumable resource which is homogeneous (genetically, chemically, or structurally) relative to the surrounding matrix; (ii) that hosts a discrete multitrophic community with species that cannot replicate solely in any of the surrounding matrix; and (iii) cannot maintain a balance between depletion and renewal – which in turn prevents the resource from supporting multiple generations of consumers or reaching a community equilibrium.

Our definition of the ERP concept (Table 2) includes a wide variety of decomposing consumable resources, in line with Beaver (1977); these resources range from animal carrion, to rotting fungi, decomposing plant matter, and animal dung (Table 3). However, it also extends to any finite organic or inorganic consumable resources that have limited means of balancing depletion and renewal and cannot support multiple generations of the same communities. This includes microscopic nutrient patches in marine and soil systems

Table 2. Factors that define an ephemeral resource patch (ERP). The resource should meet all ‘ephemeral’ and ‘patch’ criteria, and at least one ‘resource’ criterion.

Ephemeral	Unable to form a community equilibrium (Beaver, 1977) Cannot support multiple generations of taxa in the same community (Beaver, 1977) Cannot balance depletion and renewal – i.e. can be completely used up.
Resource	Consumable organic material (plant and animal tissue, fungi, dung, plankton) Inorganic energy source (nitrogen, sunlight, water)
Patch*	Homogeneous area that differs from the surrounding matrix (Forman, 1995). Homogeneity can be in a genetic, chemical, or structural context. Discrete multitrophic community assemblage with species that cannot replicate solely in any of the surrounding matrix of differing composition or structure (Forman & Godron, 1981)

*The notion of a patch can depend on both the spatial and temporal scales relevant to the focal organism(s) and the question being asked (Pringle *et al.*, 1988).

Table 3. Specific examples of resources that we consider ephemeral resource patches (ERPs) and intermediate examples according to our definition (Table 2). We distinguish three major forms: necromass, biomass, and inorganics – each of which contains several types of ERPs. These ERP ‘types’ can be divided further into ‘subtypes’; for example, ephemeral pools can form in soil depressions (puddles), within pitcher plants, and within treeholes – each of which will differ slightly in their spatiotemporal characteristics and community compositions.

Form	ERP type	Subtype	References
Necromass	Animal carrion	Terrestrial	Beaver (1977); Hanski (1987); Barton <i>et al.</i> (2013a)
		Aquatic	Pechal & Benbow (2016); Benbow <i>et al.</i> (2020)
	Animal dung	Terrestrial	Doube (1987); Finn & Giller (2000); Sladeczek <i>et al.</i> (2013)
		Aquatic	Dawson <i>et al.</i> (2016); Stears & McCauley (2018)
	Intertidal wrack	Marine	Porri <i>et al.</i> (2011); MacMillan & Quijón (2012); Heerhartz <i>et al.</i> (2016); Hyndes <i>et al.</i> (2022); Le Grice <i>et al.</i> (2022)
		Freshwater	Harris <i>et al.</i> (2014)
	Leaf litter	Terrestrial	Ponge (1991); Gołębiewski <i>et al.</i> (2019)
		Aquatic	Graça (2001); Mancinelli <i>et al.</i> (2007)
	Decomposing fruit	Terrestrial	Atkinson & Shorrocks (1984); Atkinson (1985); Rohlf & Hoffmeister (2004)
		Aquatic*	
Decomposing fungi	Terrestrial	Brabcová <i>et al.</i> (2016); Maillard <i>et al.</i> (2020)	
	Aquatic*		
Coarse woody debris [†]	Terrestrial	Vasconcellos <i>et al.</i> (2010); Cheesman <i>et al.</i> (2017)	
	Aquatic	Gurnell <i>et al.</i> (1995); Braccia & Batzer (2001)	
Biomass	Microscale nutrient patches	Terrestrial	Ettema & Wardle (2002)
		Aquatic	Mitchell <i>et al.</i> (1985); Stocker <i>et al.</i> (2008)
	Parasitic galls	—	Compton & Hawkins (1992); Sanver & Hawkins (2000); Head (2008); Duthie (2013); Forbes <i>et al.</i> (2016)
		Terrestrial	De Moraes & Mescher (2005); Amarasekare (2000)
	Parasite hosts [†]	Aquatic	Joe <i>et al.</i> (1965); Esch & Fernandez (1994)
		Terrestrial	Worthen (1989); O’Connell & Bolger (1997a); Takahashi <i>et al.</i> (2005); Pöldmaa <i>et al.</i> (2016); Maurice <i>et al.</i> (2021)
	Fungal fruiting bodies	Aquatic	Hibbett & Binder (2001)
		—	Cates & Orians (1975); Feeny (1976); Rhoades & Cates (1976)
	Ephemeral plants [†]	Pitchers [†]	Rasic & Keyghobadi (2012)
		Tree holes [†]	Sota <i>et al.</i> (1994)
Inorganics	Ephemeral pools [†]	Puddles	Blaustein & Schwartz (2001); McLachlan & Ladle (2001); Cabrera-Guzmán <i>et al.</i> (2013)
		—	Zeglin <i>et al.</i> (2011); Siebers <i>et al.</i> (2020)
	Ephemeral streams [†]	—	

*We were unable to find any literature related to the communities of these ERP subtypes.

[†]Categories that may be ERPs or non-ERPs (i.e. ‘intermediate’, see Fig. 2) according to the context of the organisms or communities in question.

(i.e. micro-ERPs) (Stocker *et al.*, 2008), many types of living fungal sporocarps (Lacy, 1984; Worthen, 1989), parasitic galls (Head, 2008; Duthie, 2013; Forbes *et al.*, 2016), some ephemeral plants (Rhoades & Cates, 1976), nutrient-rich ephemeral puddles (Blaustein & Schwartz, 2001), and some ephemeral (but not intermittent) streams (e.g. Siebers *et al.*, 2020). Akin to decomposing ERPs, these resources are all relatively homogeneous compared to their surrounding matrix, finite, depleting, and are exploited by diverse multitrophic communities – but cannot support multiple generations of those same communities or form a community equilibrium and so fall under our ERP concept.

The definition we provide does, however, exclude large inorganic resources such as intermittent/ephemeral rivers, intermittent/ephemeral ponds, and some types of ephemeral pools (e.g. pitchers, rock pools, tree-holes). Such resources, although finite, often provide a relatively stable balance

between depletion and renewal, due to predictable hydroperiods which enable them to support multiple generations of the same communities – primarily due to organismal aestivation between hydroperiods (DeWitt, 1955; Dietz-Brantley *et al.*, 2002; O’Neill *et al.*, 2016). These resources are also often large enough to contain their own heterogeneous mix of smaller scale resources and unique ERPs – including fungi, leaf litter, and animal carrion. Our definition also excludes consumable resources such as long-living plants, highly recalcitrant parts of fallen trees, live animals (including insect swarms), and animal nests – which can be extinguished, but usually persist long enough (by maintaining a balance between depletion and renewal) or are renewed so frequently that they can support multiple generations of the same communities. In cases where a living organism does not persist for long enough to support multiple generations, they often have defensive mechanisms to

deter consumers (and thus can balance depletion and renewal) – such as highly specialised defensive compounds, immune systems, or behavioural and phenotypic adaptations for avoiding consumers – restricting the possible diversity of species that can exploit them. However, this is not always the case, particularly for hosts of invertebrate parasites which can be exploited by diverse communities of generalists and specialists alike and share many characteristics with ERPs (De Moraes & Mescher, 2005; Brian & Aldridge, 2021; Hood *et al.*, 2021).

Because resources vary along these continuous gradients, it will not always be possible to demarcate a resource clearly as either an ERP or non-ERP (Fig. 2). Many non-ERPs such as tree holes, rock pools, and long-lived parasite hosts may still exhibit some ERP characteristics – particularly when the focal consumers are unable to aestivate or produce successive generations in the same host. For example, some host–parasite interactions (e.g. many Lepidoptera–Hymenoptera systems: De Moraes & Mescher, 2005) are short lived, consist of multitrophic endo-parasitoid communities, and only support a single parasite generation, and thus fit well within the ERP concept. However, other host–parasite interactions [e.g. the cladoceran host *Daphnia* and its bacterial parasite *Pasteuria ramosa* (Ebert, 2005); or human hosts and the louse *Pediculus humanus* (Nuttall, 1917)] might support multiple parasite generations and are better contextualised as classical host–parasite dynamics (Decaestecker *et al.*, 2007). Importantly, much of the theory we develop below can still be applied to these non-ERP and intermediate examples, but they should be considered on a case-by-case basis and in the context of the organisms or communities in question.

III. THE SPATIOTEMPORAL VARIABILITY OF EPHEMERAL RESOURCE PATCHES

While generally united by being short-lived and unpredictable patches, ERPs can otherwise vary greatly, from a large whale carcass to that of a mouse, or from transient leaf litter to the enduring woody debris scattered on the forest floor. This heterogeneity within and among ERPs lies at the heart of ecosystem dynamics and drives the complex evolutionary processes that shape consumers. To understand these processes, we must consider whether some types of ERP are more variable than others, and whether these differences are inherent to the structural properties of the resource or whether they arise primarily through resource \times environment interactions. Such variation will shape the evolutionary landscape and ecological constraints experienced by consumers.

Variation in ERPs can be considered at two different spatial scales – the resource patch scale (local scale) and the resource landscape scale (metapopulation scale). Careful consideration of the differences between these scales is essential, as eco-evolutionary processes can differ substantially between them (Hanski, 2012; Richardson *et al.*, 2014;

Masier & Bonte, 2020). Issues of scale with regard to eco-evolutionary theory have been well discussed elsewhere (e.g. Grünbaum, 2012; Chave, 2013; Estes *et al.*, 2018). In brief, at the patch-scale, each individual patch will have unique characteristics including size, shape, ephemerality, and compositional heterogeneity – all of which collectively shape local community composition within the patch, inter-specific interactions, and microevolutionary outcomes. At the landscape-scale, the combined characteristics of individual patches leads to emergent inter-patch properties such as spatial distribution, density, and variance, which play distinct roles in shaping the composition of the metacommunity and driving evolutionary outcomes over time.

We must consider, however, that the perceived spatiotemporal properties of ERPs will be constrained by the evolutionary history and adaptive potential of consumers (i.e. consumer view or *Umwelt*; Manning, Lindenmayer & Nix, 2004). This consumer view depends upon species-specific life histories, habitat boundaries, and resource continua (Pringle *et al.*, 1988; Levin, 1992; Hanski, 1998; Manning *et al.*, 2004; Clobert *et al.*, 2009). For example, two species may be morphologically and functionally similar, and experience the same spatial scales, but exhibit entirely different costs of movement, growth rates, dietary breadths, and reproductive strategies (Tucker, 1970; Visser *et al.*, 2016; Yukawa *et al.*, 2019). This also extends to behaviour – with phylogenetic constraints restricting the adaptive space of behavioural traits related to dispersal, resource location, and exploitation (Clobert *et al.*, 2009; Holekamp, Swanson & Van Meter, 2013; Stevens *et al.*, 2014; Venkateswaran *et al.*, 2017). Due to these inherent physiological and behavioural restrictions, no two species will be identical in how they experience the abundance, spatial distribution, and predictability of resources (Sevenster & van Alphen, 1993).

To provide an example, we can compare two insect species that both specialise exclusively on carrion. One is a fly (a strong disperser) and the other an ant (a relatively poor disperser). A large animal carcass close to the ant nest will be experienced as a highly patchy resource to the ant species, as they are only capable of foraging over a small spatial extent and are unlikely to encounter successive carcasses frequently. By contrast, an animal carcass may be perceived as a relatively continuous resource to the fly species, which can forage over a much wider fraction of the landscape, disperse easily, and will thus have a higher likelihood of encountering other carcasses. These evolutionary constraints mean that selective pressures will differ substantially between these species, even when they exploit the same type of ERP. Selection on the ants may favour wider dietary breadth (generalisation), more efficient resource tracking, or slower (and more energetically efficient) life histories. Selection on the fly may favour faster life histories, growth rates, and reproduction so that reproductive rates can be maximised across multiple resources. The same will be true when comparing selective pressures between life stages – for example between adult blowflies (which can disperse easily between carcasses) and

their larvae (which are constrained to individual carcasses). Thus, if we are to understand how ERPs shape evolutionary and ecological processes, we cannot simply rely upon objective measurements of spatiotemporal properties – but must contextualise them within the phylogenetic constraints and adaptive trait spaces of consumers (Hanski, 1998; Manning *et al.*, 2004; Evans, Wallman & Barton, 2020).

Characterising how this variation within and among ERPs, spatial scales, and resource and consumer views influences organisms and communities is central to understanding evolutionary trajectories and the structure and function of ecosystems. The first step towards this is to characterise and articulate the spatiotemporal parameters of resources. While many authors have considered variation in resource patchiness (Forman & Godron, 1981; Turner, 1989; Li & Reynolds, 1995; Wu & Loucks, 1995; Gledhill, James & Davies, 2008), ephemerality (O'Connell & Bolger, 1997b; Grünbaum, 2012), and predictability (Lacy, 1984; Worthen & McGuire, 1990; Subalusky & Post, 2019) at both the patch and landscape scales (Forman & Godron, 1981; Levin, 1992; Grünbaum, 2012; Abrahms *et al.*, 2021), and in the context of consumer perspectives (Levin, 1992; Manning *et al.*, 2004), the theory has never been applied to the full spectrum of ERPs and some parameters of patch- and landscape-scale variation have not been clearly defined: for example, ephemeral resource 'recurrence intervals' (i.e. how frequently and repeatably ERPs recur in a given landscape through time) and 'resource heterogeneity' (i.e. the structural and chemical diversity of ERPs and how they vary among patches and through time, where distinctions must be made between within-patch heterogeneity, inter-patch differences in patch heterogeneity, and the heterogeneity of the spatial distribution of patches throughout landscapes). Importantly, these spatiotemporal characteristics can be directly quantified and used to parameterise models, providing conceptual foundations that link the quantification of spatiotemporal properties with predictions of ecosystem dynamics. Such theory will be central to the management and conservation of ecosystems.

In the following two sections, we outline the spatiotemporal parameters of ERPs at both the patch (Section IV) and landscape scale (Section V) and provide conceptual illustrations for each characteristic (Fig. 3).

IV. PATCH-SCALE CHARACTERISTICS

The larval stages of many holometabolous animals are confined to patches – such as fungus gnat larvae in sporocarps, anuran tadpoles in temporal puddles, and beetle larvae in carrion. Understanding the microevolutionary outcomes of kin selection, competitive interactions, and coexistence among these organisms requires consideration of patch-scale processes (Beaver, 1977). We suggest that ERPs can be described by four spatiotemporal characteristics: volume and shape (Fig. 3A), ephemerality (Fig. 3B), community structure (Fig. 3C), and heterogeneity (Fig. 3D).

(1) Patch volume and shape

Volume and shape relate to the spatial dimensions of the resource (Fig. 3A) which represent the quantity of biomass. As patch size increases, the resource can support more individuals and a greater diversity of species (Kneidel, 1984a; Razgour, Korine & Saltz, 2010; Schmack *et al.*, 2020). Patch size can also correspond with resource heterogeneity – larger patches may have more internal micro-niches (Forman & Godron, 1981; Anusa, Ndagurwa & Magadza, 2012), which can influence the abundance and diversity of species on a patch. Likewise, patch shape can play an important role in driving community dynamics, particularly through the effect of patch shape on edge effects (Forman & Godron, 1981; Forman, 1995).

(2) Patch ephemerality

Ephemerality relates to the transformation and loss of energy from the resource over time (either due to environmental degradation or consumption) and can be considered the duration for which at least one species can consume the resource to depletion – i.e. the total energetic availability (Fig. 3B). Patch ephemerality will be influenced by various abiotic factors including temperature, humidity, wind, and light exposure (Vindstad *et al.*, 2020). For example, carrion patches are consumed more quickly at higher temperatures (Dawson *et al.*, 2021). However, there are also complex feedbacks between patch ephemerality and biotic factors such as consumer load – i.e. the more individuals there are, the faster the resource will be depleted (Subalusky & Post, 2019).

Most simply, the total time period of energetic availability can therefore be represented by three factors: \bar{x}_a , the intrinsic properties of the resource (e.g. average longevity based on mass and chemical composition), E the extrinsic abiotic properties of the environment (e.g. temperature and humidity), and c the consumer load of the resource (e.g. consumer abundance and species richness). Lastly, t represents the total time period measured, which must be standardised to compare rates of energy loss among resources.

$$\text{Ephemerality} = \frac{\bar{x}_a - (E \cdot c)}{t} \quad (1)$$

(3) Patch community structure

Every ERP hosts a multitrophic community of interacting organisms (Fig. 3C) which can be measured in three ways – species abundance, species richness, and species identities. Species abundance refers to the total number of individuals of each species within the patch. Species richness is the number of different species within the patch. Species identities change over time and define successional stages that arise from changes in the properties of the resource as it is consumed, which can enhance the capacity for certain species to colonise and survive – for example, the colonisation of

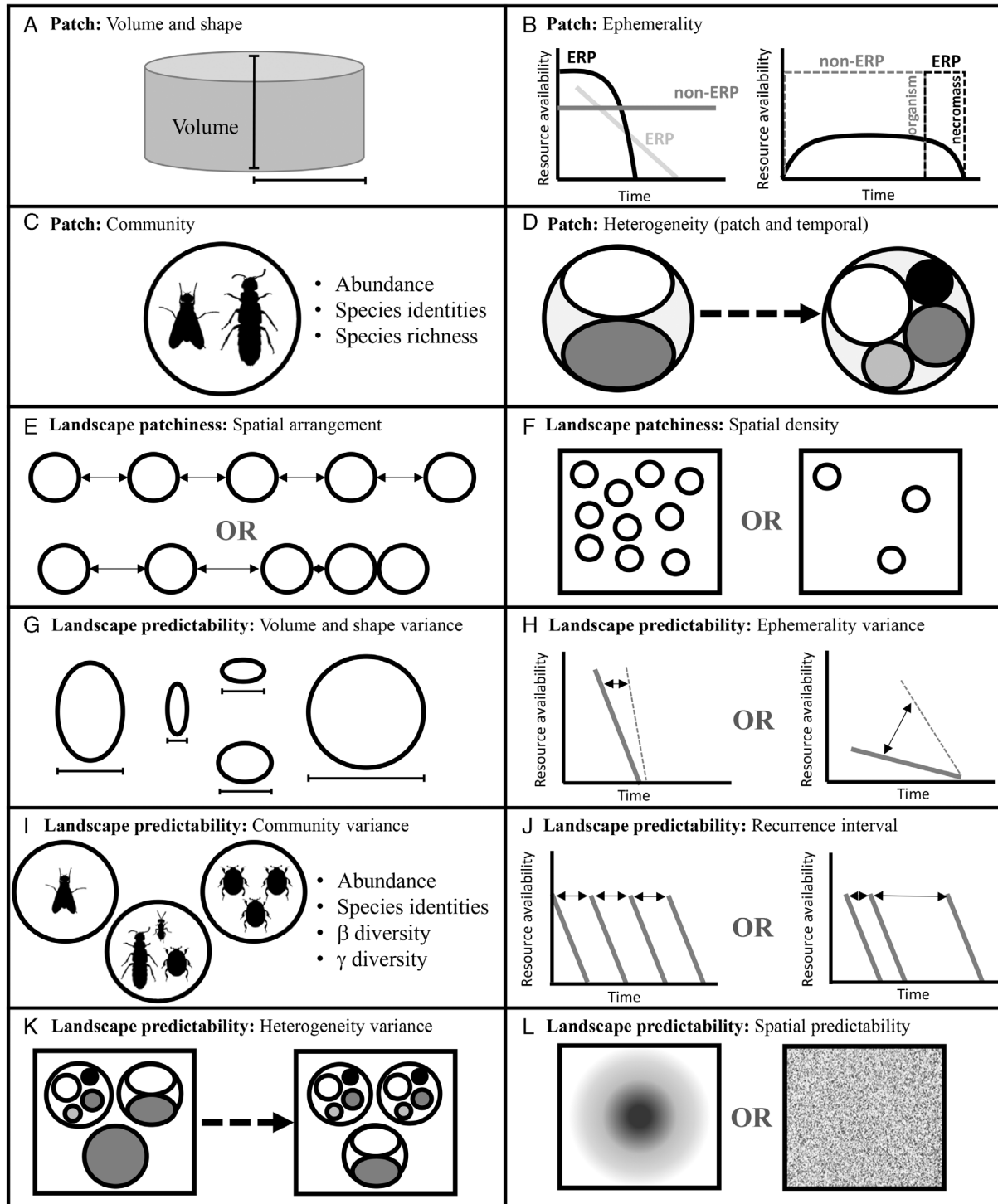


Fig. 3. The 12 major characteristics that unite ephemeral resource patches (ERPs) at different spatial scales. (A–D) At the patch scale there are four parameters. (A) Volume and shape: the spatial dimensions of the patch. (B) Ephemerality: how long the resource persists and can be consumed. The graph on the left represents resources of varying ephemerality and the graph on the right represents the energetic transition of a living organism (non-ERP) to necromass (an ERP). (C) Community structure: the abundance, diversity, and species identities of the patch community. (D) Heterogeneity: the structural and chemical diversity of the patch, and the number of distinct niches; arrow represents changes over time. (E, F) At the landscape scale, there are two patchiness parameters. (E) Spatial arrangement: the variance in distance between resources in a defined landscape. (F) Spatial density: the number of resources in a defined landscape. (G–L) At the landscape scale there are six predictability parameters. (G) Volume and shape variance: the extent (Figure legend continues on next page.)

rotting fruit by *Drosophila* flies is heavily dependent on the initial presence of yeast species (Morais *et al.*, 1995).

Importantly, perceptions of community structure and realised benefits and disadvantages to individuals using the resource are consumer specific. For example, in the presence of species A, the fitness of species B (a competitor) will be reduced, while the fitness of species C (a mutualist) will be enhanced. Thus, increased species richness and abundance, and subsequent priority effects, can be beneficial for some species through facilitation (Komo *et al.*, 2019), while being detrimental for other species through increased competition or predation (Brundage, Benbow & Tomberlin, 2014; Dawson *et al.*, 2022a). Generalist consumers, such as the Australian carrion muscid *Australophyra rostrata* (Dawson, Barton & Wallman, 2020; Dawson *et al.*, 2022b), may be able to tolerate a broad range of species compositions, whereas specialist consumers often depend on the presence/absence of certain species (i.e. arrival before predators or competitors, or after mutualists) to enhance their chances of survival (Morais *et al.*, 1995; Brundage *et al.*, 2014; Dawson *et al.*, 2022a).

(4) Patch heterogeneity

Patch heterogeneity relates to diversity in the structural and chemical composition of the resource. Higher heterogeneity generally represents a greater diversity of niches or ‘microsites’ that are available within the ERP and as it changes through time (Fig. 3D) (Shmida & Wilson, 1985). For example, aquatic leaf packs are highly heterogeneous; each leaf in the pack may come from a different tree species with a unique chemical and structural composition. These different leaf ‘microsites’ within the leaf pack will support different communities, depending on the unique physiological attributes and preferences of the consumers (Graça, 2001). Likewise in ephemeral puddles, physical crevasses can create differences in micronutrient diversity (Baskin, 1994) and provide distinct chemical niches for microbes (Muscarella *et al.*, 2019) – the number of which can vary depending on the pool’s abiotic characteristics including shape and size (Anusa *et al.*, 2012; Dalu *et al.*, 2017).

Higher resource heterogeneity usually corresponds with higher species richness due to an increased number of spatial niches within the patch (Finn & Giller, 2000; Brian & Aldridge, 2021). However, patches also vary in heterogeneity through time. For example, the initial microbial communities within leaf-pack patches are dominated by only a few select

species that can break down the recalcitrant structural (e.g. lignin) and defensive chemical compounds (Graça, 2001; Newman, Liles & Feminella, 2015). Once these structural defences are removed, a variety of niches become available – in turn increasing biotic heterogeneity and community diversity (Newman *et al.*, 2015).

From a consumer perspective, perceived heterogeneity will depend on species-specific resource breadth and continua. For generalists with adaptations that enable feeding on various nutrient and tissue types, a patch may seem entirely homogeneous whereas specialists may only be capable of feeding on a small part of the resource and perceive multiple discrete niches. Therefore, while species richness can provide a general measure of heterogeneity (i.e. the number of niches within a resource), this will not always be accurate, particularly when generalists predominate. Alternatively, resource heterogeneity can be measured by the overall diversity of micronutrients (i.e. the diversity of organic compounds containing nitrogen and phosphorous) as has been done to quantify resource heterogeneity within lakes (Muscarella *et al.*, 2019).

V. LANDSCAPE-SCALE CHARACTERISTICS

The landscape-scale concept is useful when considering the eco-evolutionary dynamics of traits, life stages, species, or metacommunities that experience selection on broader spatial scales. For example, selection on dispersal, resource tracking, and metapopulation dynamics are concepts that must be considered at the landscape scale. We suggest that resource landscapes can be described by eight characteristics, which can be classified under two broad concepts: landscape patchiness (Fig. 3E, F) and landscape predictability (Fig. 3G–L). It is the combination of all these characteristics that creates landscape heterogeneity. Importantly, because landscapes can be conceptualised at a range of scales, these landscape-scale characteristics will depend largely on the boundaries and spatial extent defined by the observer (Fig. 4).

(1) Landscape patchiness

Patchiness is a measure of spatial variance – that is, how resource patches are distributed through space relative to unusable matrix. In terms of communities, patchiness

(Figure legend continued from previous page.)

of variance in size and shape of a resource type throughout a landscape. (H) Ephemerality variance: variation in resource ephemerality throughout landscapes, a resource type on the left representing low variance and a resource on the right representing high variance. (I) Community variance: how resource types vary in their communities throughout landscapes, where different resource types may have different extents of variation in abundance, species identities, and diversity. (J) Recurrence interval: variation in how frequently and repeatably the resources recur within a given landscape. (K) Heterogeneity variance: how groups of resource patches vary in their heterogeneity throughout landscapes and through time, arrow represents changes in heterogeneity between patches through time. (L) Spatial predictability: how resources vary in spatial location through time. Resources can occur predictably at the same locations or can occur more randomly throughout a landscape.

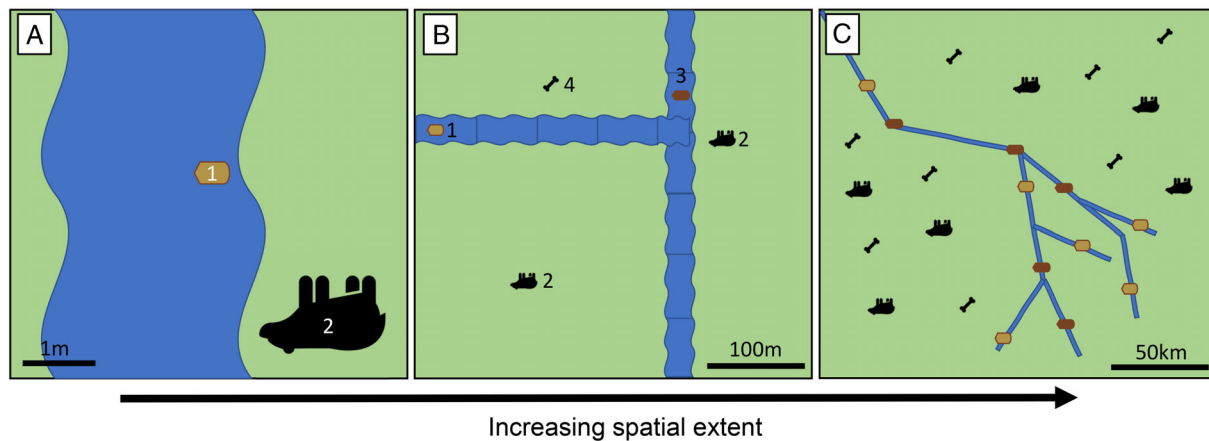


Fig. 4. Increasing spatial extent will influence how species perceive (and how researchers measure) landscape-scale patchiness, ephemerality, heterogeneity, and the recurrence interval of ephemeral resource patches (ERPs). (A) At small spatial scales patchiness is high as there is only one resource of each type available (1, an aquatic leaf pack; 2, an animal carcass), landscape resource heterogeneity is low as there are only two types of resource, and predictability is low as there is only a small area for resources to recur. (B) At intermediate scales, patchiness is high, heterogeneity is moderate as there are more resources available (3, leaf litter in late stages of decomposition; 4, an animal carcass in late stages of decomposition), and predictability is moderate as there is a larger area for resources to recur. (C) At large spatial scales, patchiness decreases as more resources of the same type are available, landscape resource heterogeneity increases as a greater diversity of resources are available, and predictability increases as there is a much greater likelihood of the same resource types recurring through the landscape.

provides a template for diverse interactions between competing species and increasing resource patchiness generally promotes increased beta diversity (among-patch differences in species diversity) and gamma diversity (landscape-wide species diversity) (O’Connell & Bolger, 1997a; McGranahan *et al.*, 2018). We suggest that patchiness can be conceptualised by two primary characteristics: spatial arrangement (Fig. 3E) and spatial density (Fig. 3F).

(a) Spatial arrangement

The concept of spatial arrangement considers how resource patches are distributed throughout landscapes (Li & Reynolds, 1995). Many ecological resources (particularly ERPs) will be spatially heterogeneous throughout landscapes, meaning that patterning trends towards random, and the variance in distance between resources is high (Fig. 3E). By contrast, spatially homogenous resources will show repeatable patterning, and will have low variance in inter-resource distances. Spatially homogenous resource landscapes generally increase the likelihood of encountering resource patches at any point in space, which will have important consequences for consumers (discussed in more detail in Sections VI and VII).

(b) Spatial density

Spatial density is simply the total number of resources within a defined landscape. We suggest that the concept of spatial density differs slightly from that of spatial arrangement – patches may be homogeneously scattered throughout two landscapes, but one landscape can still differ in density compared to the other (i.e. total number of resources) (Fig. 3F).

However, if we consider two species that experience the same spatial extent, then at extremely high spatial densities, the arrangement will trend towards homogeneity. Spatial density cannot, however, be directly compared between species that differ in their perception of spatial extent – and must be contextualised with the dispersal capacity and spatial extent of the focal species.

(c) Measuring resource patchiness

Landscape patchiness shapes community patterns and exerts selective pressures on species (Pickett & White, 1985; Hanski, 1987). As a conceptual starting point, patchiness should be measured for individual types of ERPs within a defined landscape boundary by incorporating spatial arrangement, resource size, and resource density. If σ_d^2 represents spatial arrangement (the variance in distance among resources), \bar{x}_s represents resource size (the average size of the resources), and n represents resource density (the number of individual resources in a defined landscape), then

$$\text{Patchiness} = \frac{\sigma_d^2 \cdot \bar{x}_s}{n} \quad (2)$$

(2) Predictability

Predictability is a measure of spatiotemporal variance in resource characteristics that exerts a strong selective pressure on species and has resulted in the evolution of various dispersal syndromes, behavioural adaptations, and bet-hedging strategies. The extent of resource predictability directly

impacts the pressure for specialisation: short-lived and unpredictable resources are expected to be exploited more efficiently by generalists, whereas highly predictable resources often drive the persistence of specialists (Kneidel, 1984a; Worthen & McGuire, 1990; Põldmaa *et al.*, 2016).

Importantly, perceived predictability will differ among species depending on their unique sensory physiologies and behavioural adaptations (e.g. migration patterns). Predictability may even differ among eusocial and asocial species and between young and mature adults; older animals have time to adapt behaviourally and learn search patterns from conspecifics (e.g. learned migratory behaviours in birds) (Mueller *et al.*, 2013; Pettit *et al.*, 2013). We suggest that ERP predictability can be conceptualised through six characteristics: volume and shape variance (Fig. 3G), ephemerality variance (Fig. 3H), community variance (Fig. 3I), recurrence interval (Fig. 3J), resource heterogeneity variance (Fig. 3K), and spatial predictability (Fig. 3L).

(a) Variation in volume and shape

Throughout a landscape and through time, ERPs will differ substantially in volume and shape (Fig. 3G). Some resource types will vary more in volume than others and will thus exert different selective pressures on their constituent consumers. Generally, larger ERP types will be more stable and predictable, which in turn will lead to less variation in competitive interactions, and increased fitness of specialists (Kneidel, 1984b). As an example, animal carrion varies greatly in size from the carcasses of whales to those of insects. Many species employ generalist strategies to exploit carrion of a wide range of sizes (Beaver, 1977), whereas others specialise exclusively on larger carcasses (Kneidel, 1984b). The larvae of the Australian blowflies *Calliphora augur* and *C. stygia* exemplify the generalist strategy, and can be found in dead snails, small birds, as well as large mammal carcasses (Erzincliglu, 1987; Day *et al.*, 2021) – and have likely evolved a range of adaptations to facilitate this.

(b) Variation in ephemerality

ERPs vary greatly in ephemerality throughout landscapes (Fig. 3H) depending on the unique structural and chemical characteristics of the resource and the environmental conditions (e.g. season, weather events, temperature). For example, we may expect littoral ERPs (e.g. seaweed wrack) to exhibit higher ephemerality variance (i.e. lower predictability) throughout landscapes compared to terrestrial resources (e.g. leaf litter). This is because the ephemerality variance of littoral resources is not only determined by resource size, community composition, wind, and temperature, but is also susceptible to factors such as tides and storms that can quickly redistribute or remove the entire wrackbed (Butlin & Day, 1989). Throughout a landscape, different beaches will also experience different degrees of erosion, tidal ranges, and wave frequencies depending on their geographic

location and orientation (e.g. Hyndes *et al.*, 2022). The resulting complex environmental variation among beaches will further amplify ephemerality variance of littoral ERPs throughout landscapes. Thus, we may expect littoral ERPs to exert unique selective pressures on their consumers relative to other terrestrial resources (Hyndes *et al.*, 2022) and for this to be reflected in the ecology of their communities. Higher levels of ephemerality variance throughout landscapes are generally expected to promote higher levels of beta and gamma diversity (Worthen, 1989; Daniel *et al.*, 2019) and may also promote evolutionary strategies such as adaptive tracking or bet-hedging to balance reproductive output against the unpredictable nature of the resources (discussed in more detail in Section VI).

(c) Variation in community structure

The exceptional structural and chemical diversity of ERPs provides a mosaic of niches within landscapes for many species, causing ERPs to differ in their attendant community composition throughout landscapes and through time (Fig. 3I). This landscape-level variation in community composition is a function of the spatiotemporal attributes of each patch (i.e. size, heterogeneity, patchiness, and ephemerality) but is also related to the abiotic properties of the landscape (e.g. temperature, habitat type, season, time of day) (Trumbo & Bloch, 2002; Arias-Robledo, Stevens & Wall, 2019).

To understand community variance for any one resource type, we can quantify variance in beta diversity (the extent of among-patch differences), gamma diversity (the extent of landscape-wide metacommunity diversity), species abundance, and species identities. Variance in species identities simply relates to whether community composition and ecological succession is synchronised throughout a landscape, or whether each patch of the same type tends to vary greatly in its attendant species at a given point in time. To provide a hypothetical example of low variance in species identities, we can consider a synchronised resource pulse. At small spatial scales of a few hundred metres, after a prolonged dry period and a subsequent rainfall event, ephemeral puddles will be synchronously filled, providing consumers with a relatively even selection of resources. Although some of these puddles will differ in size/shape/heterogeneity, we might expect relatively low variation (on average) in community composition among patches – because each patch becomes available at the same time. If we then increase the spatial extent (Fig. 4) to include puddles that were not filled by the rainfall event, the community structure among patches (i.e. variance in species identities) will be more asynchronous, and the perceived heterogeneity of the landscape will increase.

While it is likely that these patterns have important implications for metacommunity dynamics, many questions remain regarding differences in community composition among resource types. For example, do ephemeral puddles show lower variance in community composition after rainfall events compared to other resource types? How does variance in community composition drive local adaptation in

consumers (Yamamichi *et al.*, 2020)? Answering such questions will provide valuable insights into how ERPs shape metacommunities.

(d) *Variation in recurrence interval*

Resources that are finite must also vary in how frequently and repeatably they recur through time (Fig. 3J). For example, on small spatial scales of a few metres, leaf packs in river streams may only occur once every few weeks, but on larger spatial scales of several hundred metres they may occur continuously (Fig. 4). This ‘recurrence interval’ will have consequences for the evolution of organisms and communities, as resources that recur predictably and frequently (e.g. some mushroom types) (Worthen & McGuire, 1990) allow organisms to synchronise their development and emergence patterns seasonally and at times of peak resource abundance. Resources that recur following more stochastic patterns force organisms to evolve different strategies depending on resource availability, for example, the evolution of developmental plasticity in many desert-breeding animals where the timing of embryonic or larval development can respond to environmental conditions (Shine & Brown, 2008). High variance in the recurrence interval may even drive the evolution of more plastic traits in species (Richter-Boix, Tejedo & Rezende, 2011; Van Buskirk, 2002), which may have consequences for how ERP-breeding species respond to future climate change. Short recurrence intervals may also prime communities for subsequent resource pulses (Subalusky & Post, 2019).

Importantly, recurrence characteristics will also be consumer specific as for a given resource type, species that tend to traverse small spatial scales such as ants will experience resource recurrence as less frequent than those that traverse large spatial scales such as blowflies, given the assumption that their resource-tracking capabilities are equal. These differences between spatial scales necessitate careful consideration of how resources recur in the context of landscape characteristics and dimensions and how these relate to the community or species in question. This aligns with resource wave phenology theory outlined by Armstrong *et al.* (2016) which provides an important framework for understanding how more mobile consumers may perceive the abundance and ephemerality of resources throughout landscapes.

(e) *Variance in resource heterogeneity*

Because of their finite and depleting nature, the structural and chemical composition of ERPs will differ among patches, and the extent of these among-patch differences will change through time. Landscape-scale variance in resource heterogeneity therefore refers to how heterogeneity within patches differs among patches through space and time. Patches of a single resource type will vary spatiotemporally in chemical and structural composition (and thus the number of niches they provide) (Fig. 3K), and different resource types will exhibit different levels of variation. Ephemeral puddles, for example, vary greatly throughout landscapes (Blaustein & Scwhartz, 2001).

Because each puddle is held within a unique landscape depression or hole, no two pools will have the same depth, micronutrient diversity, or number of microhabitats (Fontanarrosa, Collantes & Bachmann, 2009; Vanschoenwinkel *et al.*, 2009; Muscarella *et al.*, 2019). Likewise, these characteristics will change through time, as different consumers in different patches consume, transform, and excrete resources at different rates, and as each patch is depleted at a unique rate due to its micro-climatic and environmental factors.

(f) *Spatial predictability*

Spatial predictability relates to the location of the resources through time. Resources can occur predictably at the same locations or can occur entirely randomly throughout a landscape (Fig. 3L). For example, some fungi may be highly spatially predictable for consumers on small scales, recurring in the same positions every year due to the stable patterning of plant roots and nutrients that support the mycorrhizae, as well as consistent rainfall patterns (Worthen & McGuire, 1990). Likewise, some temporary pools are spatially predictable due to the constant position of landscape depressions and tree holes (Sota *et al.*, 1994; McLachlan & Ladle, 2001), however their nutrient richness and diversity will not necessarily be the same. Conversely, resources like carrion can be comparatively much less predictable due to the movements of living animals, which are more susceptible to stochastic processes at small spatial scales (Abrahms *et al.*, 2021). The spatial predictability of resources will also vary at different times of year. For example, during rainy seasons puddles may be more spatially predictable, and likewise, carrion may be more spatially predictable during mass migration events (e.g. ungulate migrations in Africa) or summertime mass mortalities of fish and aquatic invertebrates (due to high temperatures and reduced oxygen in their habitats). These differences in space and time can have profound effects on how consumer species disperse, and track resources, and on how specialisation evolves, and will have profound influences on seasonal differences in landscape heterogeneity.

VI. ERPs SHAPE ECO-EVOLUTIONARY TRAJECTORIES

The remarkable variability within and among ERPs is the underlying force that shapes the ecological and evolutionary trajectories of their consumers. There is a substantial body of theory relevant to understanding how these eco-evolutionary forces have shaped ERP consumers and the spatiotemporal structure of their communities (Table 4), much of which has come from research on ERPs such as dung, carrion, and decaying plant matter (Beaver, 1977; Atkinson & Shorrocks, 1984; Hanski, 1987). However, there has also been theory relevant to ERPs developed from studies on non-ephemeral resources such as host plants

Table 4. Some of the major eco-evolutionary principles that apply to ephemeral resource patches (ERPs), alongside examples that relate the principle to our ERP concept.

Principle	Relation to the ERP concept	Examples	Related references
Adaptive tracking	An evolutionary strategy whereby optimal trait values change continually, and natural selection disfavors suboptimal forms that may have previously been well adapted. May be expected in ERPs that vary substantially in predictability between seasons (e.g. puddles in wet <i>versus</i> dry seasons).	Populations of the seaweed fly <i>Coelopa frigida</i> are polymorphic for a large chromosomal inversion. In summer, when the wrackbed is less frequently disturbed by storms, adaptation tracks the α allele (which favours slow development and high fertility) which increases in frequency over the β allele (which favours fast development and low fertility) (Mérot <i>et al.</i> , 2020). The β allele is presumably favoured when the wrackbed becomes less predictable.	Simons (2011); Rudman <i>et al.</i> (2022)
Bet hedging	An evolutionary strategy that generates random variation in fitness-related traits among individuals, increasing the likelihood that a subset of individuals expresses a phenotype that will be adaptive in a future environment. In fluctuating and unpredictable environments (such as ERPs) this strategy can result in higher geometric mean fitness (i.e. long-term reproductive success) despite possibly reduced arithmetic mean fitness (i.e. short-term reproductive success).	For frogs that develop in temporary pools, the hatching time of eggs within a clutch is often staggered (despite this increasing the risk of mis-timing emergence) (Mahony & Thumm, 2002; Erich <i>et al.</i> , 2015). Female salamanders that use unpredictable and unstable pond habitats for their larvae exhibit behavioural bet-hedging; depositing more larvae over a longer time period and more deposition events (Caspers <i>et al.</i> 2015).	Beaumont <i>et al.</i> (2009); Segev <i>et al.</i> (2011); Simons (2011)
Coexistence	ERPs promote species coexistence throughout landscapes because their patchy and ephemeral nature favours varied interspecific interactions and prevents any one individual species from colonising every patch.	Individual patches of animal carrion can be dominated by single species, but other species can persist through mutualistic interactions with dominant species, or by colonising other patches where competition is less intense.	Ives (1991); Wertheim <i>et al.</i> (2000); Reigada & Aguiar (2012); Yamamichi <i>et al.</i> (2020)
Complex life cycles	ERPs place divergent selective pressures on the different life stages of consumer species. Selection on larvae favours rapid growth and aggregation. Selection on adults favours strong dispersal, mate competition, and resource location.	Amphibians show convergence of tadpole body plans and divergence of adult body plans (Sherratt <i>et al.</i> , 2017), which suggests substantial differences in the selective pressures between life stages – possibly arising from differences in experienced habitat scales between life stages.	Mitra (2013); Collet & Fellous (2019); Herrig <i>et al.</i> (2021)
Delayed sexual maturation	Due to the patchy and ephemeral nature of ERPs, consumers develop within one patch (as larvae) and must then disperse to reproduce in another patch (as adults). Due to the high costs of dispersal and the emergence of siblings from the same patch, selection often drives delayed sexual maturation to save energy during dispersal and to prevent inbreeding.	The majority of ERP-breeding insects (e.g. mosquitoes, dung beetles, blowflies) exhibit delayed sexual maturation (taking 3–7 days to reach sexual maturity after reaching the adult life stage).	Thornhill & Alcock (1983); Butterworth <i>et al.</i> (2020)
Dispersal	Species that utilise ERPs are faced with constant and high pressure to	Dung beetles must sometimes disperse great distances between	Clobert <i>et al.</i> (2009); Barton <i>et al.</i> (2013b); Kubisch <i>et al.</i> (2014);

(Continues on next page)

Table 4. (Cont.)

Principle	Relation to the ERP concept	Examples	Related references
	disperse from patch to patch to continue their life cycle. The resulting dispersal syndromes are under strong selection and play a major role in shaping adaptive trajectories and community structure.	dung pats, as well as throughout entire landscapes (Roslin, 2000) which has resulted in unique selective pressures on wing morphology (Meresman <i>et al.</i> , 2020) and dispersal syndromes.	Cote <i>et al.</i> (2016); Jacob <i>et al.</i> (2019); Li & Kokko (2019)
Evolutionary diversification	Landscape and resource heterogeneity have likely been central factors contributing to rates and patterns of biological diversification. ERPs are some of the most heterogeneous resources found in nature and have played prominent roles in the trophic diversification and speciation of major biological radiations – from bacteria, to insects, and amphibians.	Evolutionary transitions between herbivory, mycetophagy, and saprophagy, are widespread throughout Coleoptera and have played major roles in the evolutionary diversification of the family (Leschen & Buckley, 2007; McKenna <i>et al.</i> , 2019; Motyka <i>et al.</i> , 2022)	Nyman (2010); Hubert <i>et al.</i> (2015); Czekanski-Moir & Rundell (2019)
Host–microbe associations	ERPs are high-quality resources that are susceptible to microbial spoilage and intense competition. ERP consumers (from bacteria to insects and amphibia) must overcome these challenges. One solution is to develop tight host–microbe symbioses which can enhance the host's capacity to consume the resource or increase the longevity or quality of the resource – to the benefit of both the host and symbiont. Such relationships are widespread throughout ERP consumers.	Midges of the tribe Asphondyliini use a needle-like ovipositor to introduce fungal conidia and eggs into the plant organs they attack. Larvae are unable to initiate the gall or to develop without their fungal associates (Rohfritsch, 2008; Kolesik <i>et al.</i> , 2019). Microbial symbionts of the burying beetle (<i>Nicrophorus vespilloides</i>) prolong the lifespan of carrion by preventing microbial succession and putrefaction – enhancing the longevity and quality of the larval resource (Shukla <i>et al.</i> , 2018).	Gould <i>et al.</i> (2018); van Vliet & Doebeli (2019)
Kin selection	Because of the highly competitive and ephemeral nature of ERPs, one evolutionary strategy is to optimise reproductive success by laying multiple offspring on the same resource. However, this guarantees competition among kin – meaning that larvae that utilise ERPs often experience strong selective pressure for positive sociality and kin selection.	<i>Drosophila</i> that breed in decaying fruit exhibit higher fitness when aggregating with related kin (Khodaei & Long, 2019).	Łukasiewicz <i>et al.</i> (2017); Li & Kokko (2019); Charabidze <i>et al.</i> (2021)
Landscape heterogeneity	The substantial spatial and temporal variability of ERPs provides an ever-changing resource landscape that promotes biodiversity and exerts a distinct suite of selective pressures on consumers driving a wide range of adaptive strategies.	Plant galls can range considerably in size, ephemerality, and heterogeneity throughout landscapes. This diversity shapes the structure of gall communities (e.g. host–parasitoid relationships) throughout the landscape (Van Hezewijk & Roland, 2003).	Turner (1989); Bump <i>et al.</i> (2009); Barton <i>et al.</i> (2013a); Shepard <i>et al.</i> (2013); Stein <i>et al.</i> (2014); Stiegler <i>et al.</i> (2020)
Metapopulation dynamics	Each ERP consists of an unstable local population, and the combination of these discrete local populations throughout a landscape is termed the	The extent of patchiness of plant galls influences the persistence of gall parasitoids in the metacommunity (Start & Gilbert, 2016). Small, isolated galls tend to contain fewer	Nee & May (1992); Hanski (1998)

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Table 4. (Cont.)

Principle	Relation to the ERP concept	Examples	Related references
Necrobiome	‘metapopulation’. Because of this hierarchical population structure, extinction of a species in any given patch does not preclude regional persistence due to the capacity to persist in multiple other patches. ERPs are exploited by a complex community of micro- and macro-organisms in various states of growth and decay. This exceptionally diverse community is termed the ‘necrobiome’ and changes greatly in community composition over time and through space.	specialist parasitoids. Such parasitoids are instead sustained in the metacommunity by larger, well-connected patches of galls. Animal dung is exploited by a complex community of micro- and macro-organisms – from bacteria, to fungi, invertebrates, and vertebrates.	Tomberlin <i>et al.</i> (2017); Brundage <i>et al.</i> (2017); Weatherbee <i>et al.</i> (2017); Benbow <i>et al.</i> (2019) Pechal <i>et al.</i> (2013); Dangerfield <i>et al.</i> (2020)
Non-equilibrium dynamics	Because ERPs go fully extinct and are colonised uniquely every time, they can never form a stable community equilibrium (although may form stable metacommunities).	Individual plant galls contain various limiting nutrients, from the tissue of the gall-inducer to the host plant tissue, symbiotic fungi, and bacteria. Once these resources are consumed, and the gall-inducer completes development (or dies) the resource becomes extinct.	Beaver (1977); Kneidel (1984b)
Parental care	Because of the highly ephemeral nature of ERPs, selection can favour strategies whereby parents enhance the survival of their offspring by facilitating feeding or protecting the resource from other competitors, predators, and parasites.	The burying beetle <i>Nicrophorus vespilloides</i> bury carrion underground, treat the carcass with secretions that prevent microbial growth, then lay eggs on the resource. Once the offspring hatch, they enter a pre-prepared opening in the resource and are fed pre-digested carrion by their parents (Smiseth <i>et al.</i> 2006).	Capodeanu-Nägler <i>et al.</i> (2018); Charabidze <i>et al.</i> (2021)
Phenotypic plasticity	The capacity of individual genotypes to produce different phenotypes over a range of environments. Given the heterogeneous and variable nature of ERPs, phenotypic plasticity is expected to be a common evolutionary outcome, although it may not always be adaptive.	Carrion- and dung-breeding flies exhibit developmental plasticity dependent upon resource quality. When the resource is abundant and competition is low, growth rates are optimised to maximise body size. When resources are limited, individuals mature earlier and at much smaller body sizes (Blanckenhorn, 1998)	Simons (2011); Murren <i>et al.</i> (2015); Acasuso-Rivero <i>et al.</i> (2019); Nilsson-Örtman & Rowe (2021)
Rapid ontogeny	The short-lived and unpredictable nature of ERPs can select for rapid development, and unique life history strategies such as viviparity.	Carrion breeding flies have evolved various developmental strategies (e.g. viviparity, larval aggregation, phenotypic plasticity) that assist with the rapid use of resources.	Levot <i>et al.</i> (1979); Charabidze <i>et al.</i> (2021); Komo & Charabidze (2021)
Resource competition	Because of the patchy, short-lived, and highly competitive nature of ERPs, species that utilise them have evolved a variety of responses to competition.	Carrion breeding <i>Chrysomya</i> flies have evolved various mechanisms to outcompete or exploit heterospecific competitors – including competitive exclusion and facultative predation (Dawson <i>et al.</i> , 2022a).	Atkinson & Shorrocks (1981); Kneidel (1984b); Jones <i>et al.</i> (2012)
Resource heterogeneity	Each individual ERP has a diverse composition of chemical and structural components – which will differ among patches and through	Temporal puddles will contain various crevasses, micronutrients, and elemental concentrations (e.g. C:N ratios). The diversity of these	Wertheim <i>et al.</i> (2000); Dalu <i>et al.</i> (2017); Muscarella <i>et al.</i> (2019)

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Table 4. (Cont.)

Principle	Relation to the ERP concept	Examples	Related references
	time as the resource is transformed by consumers and decomposes.	components will influence the diversity of consumers, and will also change through time as components are consumed, transformed, and excreted.	
Resource subsidy	ERPs are subject to boom–bust cycles, resulting in the generation of significant numbers of consumer offspring. This can have large-scale trophic effects in ecosystems (see source–sink dynamics).	Mass mortality events generate non-limiting amounts of carrion and increase the abundance of consumer species – which has important consequences for coexistence and competitive dynamics.	Polis <i>et al.</i> (1997); Murakami & Nakano (2002); Yang <i>et al.</i> (2008); Bódis <i>et al.</i> (2014); Subaluský <i>et al.</i> (2017); Lashley <i>et al.</i> (2018); Stepanian <i>et al.</i> (2020)
Resource tracking	ERP breeding species must respond dynamically to ever-changing and heterogeneous resource landscapes. Animals should therefore evolve movement patterns (e.g. non-random dispersal, migrations) dependent upon the distribution and phenology of their required resources.	Many fly species exhibit genetically determined and heritable resource searching behaviours (Collins <i>et al.</i> , 1994) which may optimise the chance of locating unpredictable resource patches or the capacity for organisms to track resource waves.	Armstrong <i>et al.</i> (2016); Abrahms <i>et al.</i> (2021)
Sensory ecology	As ERPs are patchy and unpredictable, selection drives ERP specialists to have highly efficient and reliable means of resource detection. This exerts strong selection on sensory systems (i.e. chemoreception for volatile cues from resources, hosts, and conspecifics).	Mosquito species have evolved highly specialised olfactory and visual adaptations for sensing the location of oviposition sites (Bentley & Day, 1989).	Hamilton <i>et al.</i> (2011); Brodie <i>et al.</i> (2015); Montell & Zwiebel (2016); Yan <i>et al.</i> (2018); Keckskeméti <i>et al.</i> (2020)
Sexual selection	Sexual selection depends on environmental context. The extreme stochasticity and seasonality of ERPs will drive high variability in the density, distribution, and operational sex ratios of conspecifics through space and time, all of which moderate the form and function of sexual selection. Sexual selection experienced by ERP consumers will thus vary greatly among resources, throughout landscapes, and over time. ERPs therefore create a complex selective landscape with regard to reproduction, likely resulting in a range of unique evolutionary strategies.	Fungivorous <i>Tapeigaster</i> flies (Heleomyzidae) exhibit intense male–male competition on fungal sporocarps (McAlpine & Kent, 1982). Amphibians and flies that mate in and around temporal puddles show high degrees of intrasexual competition and sexual selection [frogs (Wells, 1977; Byrne & Roberts, 2004); flies (Butterworth & Wallman, 2021)]. Carrion-breeding flies (Piophilidae and Calliphoridae) exhibit male–male competition (Bonduriansky & Brooks, 1999) and complex courtship (Butterworth <i>et al.</i> , 2019). Saprophagous <i>Teleostylus</i> flies (Neriidae) show high degrees of male–male competition and mate guarding (Wylde <i>et al.</i> , 2020).	Davies & Lundberg (1984); Reichard <i>et al.</i> (2008); Wilson <i>et al.</i> (2010); Le Grice & Holwell (2022)
Source–sink dynamics	With a high rate of propagule influx, some individuals of a species will become established in unfavourable habitats in which they have low fitness and cannot maintain viable populations. Constant immigration from regions of high habitat quality (and high	Mass mortality events will generate non-limiting amounts of carrion, producing an abundance of consumers. In turn, this will increase the likelihood that some individuals will disperse into sites where they cannot find adequate resources or maintain viable	Shmida & Wilson (1985); Kunin (1998); Amarasekare & Nisbet (2001); Mouquet & Loreau (2003)

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Table 4. (Cont.)

Principle	Relation to the ERP concept	Examples	Related references
	(fitness) prevents local extinction in unfavourable sites.	populations. These edge populations may persist as long as the resource surplus remains.	
Specialisation	ERP breeding species differ greatly in their extent of trophic specialisation – ranging from monophagous obligate specialists to polyphagous facultative generalists. Specialists are expected to have higher fitness when ERPs are highly predictable and abundant.	Several species of Australian <i>Borboroides</i> (Diptera: Heleomyzidae) are obligate specialist consumers of wombat dung (McAlpine, 2007). By contrast, Australian <i>Calliphora augur</i> (Diptera: Calliphoridae) are attracted to and can breed within a wide range of carrion from mammal carcasses to dead snails (Erzinclioglu, 1987).	Lacy (1984); Kneidel (1984b); Abrams (2006); Büchi & Vuilleumier (2014); Pöldmaa <i>et al.</i> (2016); Peers <i>et al.</i> (2012)
Succession	Because ERPs are finite and cannot balance renewal and depletion, their composition shifts over time as they are consumed and decompose. These compositional changes provide varied windows of opportunity for consumers and result in priority effects and successional patterns.	The dung of the brush-tailed possum <i>Trichosurus vulpecula</i> shows clear patterns of fungal succession, initially being colonised by a diverse community of fungi, the composition of which changes over time as the dung decomposes (Bell, 1975).	Michaud <i>et al.</i> (2015); Sladeczek <i>et al.</i> (2021)

(Janzen, 1968; Cates & Orians, 1975), and island communities (MacArthur & Wilson, 1967; Lomolino, 2000).

Bringing this theory together, it becomes clear that ERPs are distinct and integral parts of the selective canvas that collectively shape species dynamics, community patterns, and entire ecosystems. For example, the strong selective pressures stemming from the short-lived and unpredictable nature of ERPs have likely had (and continue to have) a prominent role in driving species diversification and forging new evolutionary opportunities (Vogler & Timmermans, 2012; Cai *et al.*, 2014) from bacteria to insects and amphibians. The possible origin of dung beetles is a fascinating example, where it has been hypothesised that shifts in dinosaur dung composition during the Cretaceous angiosperm boom opened a unique dietary niche for some previously strictly herbivorous scarabaeid beetles, eventually leading to an entirely coprophagous lifestyle (Gunter *et al.*, 2016). Anuran lineages also provide numerous examples of transitions from stable resources to ERPs, with comparative analyses revealing substantial divergence in habitat use from stable ponds to ephemeral puddles (Van Buskirk, 2003; Richter-Boix *et al.*, 2011; Zimkus *et al.*, 2010). ERPs have therefore clearly played a role in fostering the evolutionary diversification of major lineages, but exactly how they have shaped these trajectories remains unclear. ERPs are some of the most heterogeneous resources found in nature, and this heterogeneity has likely been a central factor driving the patterns of biological diversification of their consumers (Nyman, 2010; Zhang *et al.*, 2020). However, many questions remain at the intersection between resource heterogeneity, metacommunity dynamics, and eco-evolutionary diversification (Hubert

et al., 2015): how do we reconcile microevolutionary processes within ERPs with local adaptation throughout metapopulations, and longer-term diversification and speciation? Have trophic shifts to, or from, ERPs been associated with higher speciation rates? The spatiotemporal characteristics we outline above, and our ERP framework, together now provide the conceptual foundation for incorporating ERPs into this theory.

There are many examples where ERPs have been an evolutionary platform for transition to other trophic strategies. For example, the common ancestor of flesh flies (Diptera: Sarcophagidae) most likely bred in invertebrate carrion (Yan *et al.*, 2020), from which both parasitism and kleptoparasitism have since evolved. Flesh flies in the genus *Emblemasoma* are parasitoids of living cicadas (Schniederkötter & Lakes-Harlan, 2004). In the genera *Amobia* and *Protomiltogramma*, adults are kleptoparasites of living solitary wasps and bees (Johnston *et al.*, 2020, 2021), laying larvae inside the host nest, which is stocked with invertebrate carrion by the host. There are also examples of invertebrates that exhibit a mixture of strategies, for example the sheep blowfly *Lucilia cuprina* can complete its lifecycle by breeding in carrion or by acting as a facultative parasite of live mammals (Norris, 1959). How these transitions occur (between trophic strategies and between ERPs and non-ERPs), and the evolutionary causes and consequences, are poorly understood, however, they have the potential to provide significant insights into the evolutionary history of a wide variety of animal clades (e.g. Leschen & Buckley, 2007; McKenna *et al.*, 2019; Yan *et al.*, 2019, 2020; Bayless *et al.*, 2021). Future research could investigate whether certain taxa are over-represented as ERP consumers, whether

there are specific morphological and functional traits that increase the capacity for ERP exploitation, and if shifts to, and from, ERPs are associated with subsequently higher rates of trophic diversification.

In addition to driving divergence between species, ERPs have also played a major role in driving divergence between life stages, particularly in species that undergo complete metamorphosis. Adults and larvae of such species often experience ERPs in entirely different contexts – adults use them primarily for locating mates, laying offspring, and occasionally as a food source. By contrast, larvae use ERPs as their primary habitat (utility resource), and as essential consumable resources for growth and development. As such, the different life stages experience entirely different selective pressures from ERPs, likely contributing to the adaptive decoupling of life stages in metamorphosing animals (Mitra, 2013; Sherratt *et al.*, 2017; Collet & Fellous, 2019). The extreme stochasticity of the larval environment may also be responsible for driving increased phenotypic plasticity in larval life stages (Van Buskirk 2002, 2009; Richter-Boix *et al.*, 2011). There is much to be learned about how selective pressures within patches drive adaptations in larvae, and how these relate to genetic and phenotypic adaptations during the adult life stage which experiences greater selection at the landscape scale. There are thousands of species with complex life cycles that exploit ERPs and could be used as model systems to address questions regarding how pleiotropy is resolved between larval and adult traits, the extent to which selection on larval traits constrains adaptation in adults (and *vice versa*), and the costs of adaptive decoupling, particularly in the context of genome size and genetic baggage.

Complex life cycles are, in fact, common among animals that exploit ERPs (Wilbur, 1980), implying that metamorphosis may have facilitated the exploitation of ERPs. One crucial benefit of metamorphosis is that it enhances the capacity for coexistence through the partitioning of life history across two separate biological forms, reducing competition between conspecifics and promoting species coexistence. For example, the adults of two species can overlap in the same habitat when their larvae feed on entirely different resources, or use the same resource but with staggered seasonality, succession, or development times. This enhanced spatiotemporal flexibility, which is largely unique to metamorphosing animals, has likely played a key role in the remarkable success and diversity of various ERP consumers from flies to frogs (Truman & Riddiford, 1999; Erezylmaz, 2006; Ten Brink *et al.*, 2019).

Another crucial way that ERPs have shaped organisms is the remarkable adaptive plasticity of ERP consumers. Species that use ERPs as resources have been shown to have steeper developmental reaction norms (e.g. damselflies; Nilsson-Örtman & Rowe, 2021) and lower developmental thresholds, enabling earlier maturation (Blanckenhorn, 1998; Nilsson-Örtman & Rowe, 2021). There are also surprising examples of trophic plasticity dependent upon resource availability – with trophic shifts that occur when resources are limited – from mycophagy to predation in nematodes

(Kanzaki, Ekino & Giblin-Davis, 2019), and from saprophagy to predation in carrion-breeding blowflies (Dawson *et al.*, 2022a). All these strategies can be of substantial adaptive benefit when utilising highly variable and unpredictable resources such as ERPs, however, many key questions remain unanswered. Future work could investigate whether high levels of phenotypic plasticity are a natural prerequisite for ERP consumers, whether ERP consumers always have steeper reaction norms than their non-ERP breeding counterparts, what the costs of plasticity are and if these costs change between seasons or environments when spatiotemporal characteristics (i.e. ERP predictability) shift.

Beyond phenotypic plasticity, ERP consumers have also evolved other adaptive strategies including adaptive tracking in seaweed flies and fruit-feeding *Drosophila* (Mérot *et al.*, 2020; Rudman *et al.*, 2022), and bet hedging in fairy shrimp that inhabit temporary pools (Philippi *et al.*, 2001). Such remarkably diverse strategies highlight the key role that spatiotemporal heterogeneity of ERPs plays in driving adaptation and raise numerous questions. While there may be general adaptive trends shared among ERP consumers (i.e. the extent of bet-hedging or adaptive tracking), optimal adaptive strategies are likely vary among resource types (i.e. the spatiotemporal characteristics of seaweed wrack might select for different strategies compared to animal carrion). There is significant potential for future research – from meta-analyses correlating resource characteristics with adaptive strategies, to studying reaction norms across ERP types (e.g. for generalists such as black soldier flies) as well as within ERPs across seasons and environments. Our framework now provides the toolset to begin such work.

It is also important to link the spatiotemporal dynamics of ERPs to movement ecology. For example, the exceptional spatiotemporal heterogeneity of ERPs is linked tightly to the evolution of consumer dispersal syndromes. In general, dispersal is non-random and dependent on both individual internal factors (e.g. neurology, costs of movement, energy reserves, sex, behavioural syndromes) and environmental heterogeneity (e.g. population density, resource availability, environmental predictability, and temperature) (Rodrigues & Johnstone, 2014; Mishra *et al.*, 2018; Jacob *et al.*, 2019). We can therefore expect the high spatiotemporal variability of ERPs to exert strong selection on dispersal dynamics. For example, decreasing temporal stability of habitats has been shown to shift optimal strategies from negative to positive density-dependent dispersal (Rodrigues & Johnstone, 2014). Different types of ERPs will therefore impose unique pressures on dispersal – depending on their recurrence intervals, ephemerality variance, and spatial predictability – likely favouring different optimal strategies over time or sustaining local polymorphisms in dispersal syndromes (Jacob *et al.*, 2019). The framework we provide herein allows us to begin addressing these questions by quantifying the spatiotemporal parameters of ERPs and relating these directly to dispersal syndromes. Moving forward, ERPs will therefore provide an effective model for understanding how spatiotemporal heterogeneity in resources shapes the evolution of

dispersal, the coexistence of different dispersal syndromes, and the broader consequences for metapopulation dynamics.

The spatiotemporal heterogeneity of resources also plays a major role in shaping sexual selection (Marsh, Rand & Ryan, 2000; Borg, Forsgren & Magnhagen, 2002; Lindström, 2001; Vergara *et al.*, 2012). Despite this, studies relating environmental heterogeneity to sexual selection remain rare (Gillespie *et al.*, 2014; Miller & Svensson, 2014), particularly in the context of ERPs. We can, however, expect that a wide range of mating dynamics are likely to be influenced by the heterogeneity of ERPs. For example, male water striders inhabiting ephemeral streams have been shown to exhibit lower levels of aggression towards females (compared to their counterparts in perennial streams) due to the higher costs of local exploitation in patchy environments (Wilson *et al.*, 2010). This elegant example highlights the powerful selective pressure that ERPs can impose on consumers.

We also know that seasonality will shift the ERP landscape over time, and thus the form and function of sexual selection will also shift seasonally (Reichard, Smith & Bryja, 2008; Gillespie *et al.*, 2014). During large resource subsidies (e.g. seaweed wrack in the warmer months) the population density of consumers can increase rapidly, resulting in a higher-than-average proportion of females developing in synchrony and emerging in large numbers at the same time. It remains unclear how this widespread synchrony in the availability of receptive females influences sexual dynamics (i.e. whether there is higher or lower intrasexual competition; Ims, 1988). Likewise, during large resource subsidies, source–sink dynamics will push both sexes into regions of lower resource quality, particularly the more dispersive sex – whether such changes shift the operational sex ratio and the dynamics of sexual selection in edge habitats requires further study.

The predictability of ERPs (particularly in edge habitats) will also greatly constrain or enhance condition dependence. For example, when resources are abundant and predictable, phenotypic variance between males of different qualities will be reduced – thus high-quality males might only be distinguishable, and accrue higher reproductive fitness, during times (or within landscapes) with poor resource abundance or low predictability (Vergara *et al.*, 2012). Alternatively, selection may instead alter the correlation between phenotype and condition – and this could result in steeper condition-dependent slopes in species that utilise more unpredictable ERPs.

The patchy distribution of food resources will also change the form and direction of sexual selection – for example, in the mating system of the dunnock *Prunella modularis*, increasing levels of resource patchiness increase female flight ranges, making it harder for males to monopolise females and subsequently leading to increased rates of polyandry (Davies & Lundberg, 1984). It is possible that this relationship between resource predictability/patchiness and selective pressure could also extend to processes such as sperm competition. For example, sperm competition could be greater in regions of low spatial predictability or low resource density, when

females cannot be monopolised and can benefit from polyandry and hedging bets across multiple males. Likewise, sex allocation could be affected, with females trading off investment in offspring sex depending on spatiotemporal variance in resource abundance, ephemerality, patchiness, and predictability (West & Sheldon, 2002; Hjernquist *et al.*, 2009). Future studies could investigate the consequences on operational sex ratios of resource-poor landscapes or periods of low resource predictability.

The use of short-lived and unpredictable resources as mating sites is, however, unlikely to be the ideal strategy for every ERP consumer. In fact, many ERP-breeding species have evolved (or had evolved prior to using ERPs) to use hilltops, leks, and other landmarks as mating sites, rather than the ERPs themselves (Thornhill & Alcock, 1983; Alcock, 1987). These unique sexual dynamics will not apply to all ERP-breeding species, and future research should examine how phylogenetic constraints on mating systems have driven differences in sexual selection between ERP consumers.

Overall, ERPs have clearly left deep evolutionary footprints in the form and function of their consumers – from patterns of diversification and speciation to adaptive decoupling between life stages, metamorphosis, adaptation, plasticity, dispersal syndromes, and sexual selection. Research now needs to focus on understanding these evolutionary processes in the context of variation in the spatiotemporal ERP characteristics we outlined in Sections IV and V. This will likely reveal novel adaptive strategies, aid the development of new eco-evolutionary theory, and greatly improve our understanding of the form and function of organisms and ecosystems.

VII. A UNIFYING FRAMEWORK TO ADVANCE KNOWLEDGE OF ERPs

In the above review, we defined the spatiotemporal characteristics of ERPs, demonstrated the importance of scale and consumer perspectives, and related a considerable body of eco-evolutionary theory to the dynamics of ERPs. This substantial reframing of ERP theory provides the basis of our unifying framework (Fig. 5) aimed to guide future research in this area. We establish this framework by drawing together the key characteristics of ERPs within three main categories: patch-scale, landscape-scale patchiness, and landscape-scale predictability. We also distinguish the objective ‘resource view’ (how resources vary in space and time) from the ‘consumer view’ (how individual species and communities may differ in their perceptions of resource characteristics). We highlight the ecological and evolutionary theory that is most relevant to each attribute and outline some broad outcomes of manipulating these attributes for ecological communities.

This conceptual framework allows us to formulate explicit hypotheses about how variation within and among ERP types influences biotic communities, trophic relationships, and the structure of ecosystems. Particularly compelling

Level	Attribute	Resource view	Consumer view	Relevant concepts	Predicted outcomes
Patch	<i>Volume and shape</i>	The total volume and shape of the resource which reflects biomass	Resource volume is relative to the size, life history, and physiological constraints of each species	Edge effects, competition, developmental and phylogenetic constraints	
	<i>Ephemerality</i>	The period that the resource is energetically available to at least one species	Species specific windows of resource availability	Resource quality, resource × environment interactions, consumer load, phylogenetic constraints	
	<i>Community</i>	The abundance, richness, and species identities of the community inhabiting the resource	Species specific mutualists, competitors, predators, parasites, and windows of opportunity	Competition, exclusion, priority effects, succession, facilitation, predation, specialisation	
	<i>Heterogeneity</i>	The structural and chemical diversity of the resource – reflects the number of niches within the resource	Niche breadth, boundaries, and perceived structural and chemical diversity are species specific	Micronutrient diversity, microtopography, species richness, niche partitioning, niche breadth, specialisation	
Landscape patchiness	<i>Spatial arrangement</i>	Variance in spatial distance between resources at a given point in time within a defined landscape boundary	Perceived spatial arrangement depends on species specific resource continua and habitat boundaries	Dispersal syndromes, resource tracking, migration, competition, coexistence, community diversity, source–sink dynamics	
	<i>Spatial density</i>	The number of resources within a defined landscape boundary	Perceived spatial density depends on species specific habitat boundaries and resource continua	Dispersal syndromes, resource tracking, migration, competition, coexistence, community diversity, source–sink dynamics	
Landscape predictability	<i>Volume and shape variance</i>	The extent of volume and shape variation for a particular resource type throughout a landscape	Perceived variance in resource volume and shape dependent on species size, physiological constraints, and life history	Source–sink dynamics, landscape heterogeneity, metapopulation dynamics, competition	
	<i>Ephemerality variance</i>	The extent of variation in ephemerality for a particular resource type throughout a landscape	Perceived variance in ephemerality dependent on species specific windows of opportunity	Succession, metapopulation dynamics, bet-hedging, plasticity, resource tracking, competition, coexistence	
	<i>Community variance</i>	The variance in community composition between patches and throughout time within a landscape	Species specific community associations, and specific cues to detect community composition – for competitor and predator avoidance	Coexistence, competition, priority effects, sensory ecology, sexual selection	
	<i>Recurrence interval</i>	The variance in time until the recurrence of a resource type – depends on spatial scale	Perceived recurrence interval depends on species specific resource breadth and habitat boundaries	Dispersal syndromes, resource tracking, resource waves, phenology, adaptive tracking, bet-hedging	
	<i>Heterogeneity variance</i>	The extent of variation in resource heterogeneity for a particular resource type within a landscape	Perceived variance in heterogeneity is dependent on species specific niche breadths	Coexistence, non-equilibrium dynamics, landscape heterogeneity, specialisation, bet-hedging	
	<i>Spatial predictability</i>	The variance in the spatial location of resources through time within a landscape	Species specific habitat boundaries and means of predicting resource location	Landscape heterogeneity, specialisation, dispersal, resource tracking, bet-hedging, adaptive tracking, source–sink dynamics	

Fig. 5. The ephemeral resource patch (ERP) framework which outlines the characteristic attributes of ERPs in the context of the objective ‘resource view’ (how the resources vary in space and time), and the ‘consumer view’ (how individual species and communities may differ in their perceptions of resource characteristics). The predicted fitness outcomes are based on existing theory relating to landscape predictability (Cates & Orians, 1975; Pöldmaa *et al.*, 2016), landscape patchiness (Worthen, 1989; Jonsen & Fahrig, 1997; Gledhill *et al.*, 2008), patch size (Kneidel, 1984a; Razgour *et al.*, 2010), patch ephemerality (O’Connell & Bolger, 1997a; Rhoades & Cates, 1976), and patch heterogeneity (Wertheim *et al.*, 2000). S = ERP specialists [i.e. specialist users of ERPs which breed on a narrow range of resources, e.g. flies in the genus *Borboroides* (Diptera: Heleomyzidae) which are specialists on the dung of wombats (McAlpine, 2007)]; G = ERP generalists (i.e. generalist users of ERPs, e.g. the common house fly *Musca domestica* and black soldier fly *Hermetia illucens* which breed in a wide range of ERP types).

questions, if short-lived and unpredictable resources tend to favour generalist strategies (Denno & Cothran, 1975;

Lacy, 1984; Jonsen & Fahrig, 1997), include: (i) Why are all ERP consumers not generalists? (ii) How do specialist ERP

consumers persist? and (iii) Do certain types of ERPs support one type of specialisation strategy over the other?

Based on existing theory relating to patch- and landscape-scale characteristics, we provide some predictions as to how the spatiotemporal characteristics we propose may enable the persistence of both specialist and generalist ERP consumers (Fig. 5). For example, it is well established that decreasing predictability of resources throughout a landscape will enhance the relative fitness of generalists *versus* specialists (Lacy, 1984; Pöldmaa *et al.*, 2016), and may also influence the evolutionary pressure for consumer specialisation over time. If we assume that some ERP types are more variable in predictability than others (i.e. some may be consistently predictable, while others will vary in predictability depending on environmental conditions such as season), then resources that are highly variable in predictability will at times be predictable (favouring specialists) and at other times unpredictable (favouring generalists). As an example, we can use the predictability of ephemeral puddles throughout the wet and dry seasons. During the wetter seasons when rain is frequent, the occurrence of puddles will become more predictable (favouring specialists), but during the drier seasons when rain is less frequent, predictability will be greatly reduced (favouring generalists). Such fluctuations in seasonal resource predictability might maintain both specialists and generalists in the metacommunity. In cases where ERPs are more consistently predictable (and vary less in predictability with environmental conditions), we should expect that consistently predictable resources will support increased fitness of specialists, and consistently unpredictable resources will support increased fitness of generalists.

However, we must also consider that ecological specialisation is simply a process of adaptation to a subset of possible environments (Poisot *et al.*, 2011) (i.e. extent of local 'resource' adaptation). As such, specialisation is not binary, but rather exists as an adaptive continuum, from highly specialised monophages that feed on single ERP types (Washburn & Cornell, 1981), to polyphagous specialists that feed on multiple closely related ERP types (Pöldmaa *et al.*, 2016; Frank *et al.*, 2018), and polyphagous generalists that can feed on drastically different ERP types (Tomberlin, Sheppard & Joyce, 2005; Nguyen, Tomberlin & Vanlaerhoven, 2015). Generalists can also vary as to whether they use ERPs facultatively as an occasional consumable resource (facultative ERP generalists), or obligately as a consumer of a wide variety of ERP types from carrion to decaying vegetation (obligate ERP generalists). The degree of specialisation may also change throughout the lifetime of an organism depending on the availability of surrounding resources (Szigeti *et al.*, 2019).

Understanding the influence of even a single aspect of resource variation (e.g. variance in resource volume) on specialist or generalist communities will therefore necessitate consideration of species-specific phylogenetic constraints, adaptive potentials, reaction norms, and life histories (for an in-depth overview of specialisation theory, see Poisot *et al.*, 2011). The wide range of ERPs we have identified provide exceptional models for testing such theory and

elucidating mechanisms of adaptation and ecological specialisation. This is because ERPs can be manipulated in the field (Finn & Giller, 2000; Spencer *et al.*, 2021) and in controlled environments (Hanski, 1987; Shorrocks, 1991), and many of the species that use them can be easily reared in laboratory settings (Nguyen *et al.*, 2015; Khodaei & Long, 2019; Wylde, Crean & Bonduriansky, 2020; Day *et al.*, 2021). It is imperative that researchers begin to quantify these attributes of resources in nature, correlating diversity metrics of specialists and generalists with resource landscape characteristics (Jonsen & Fahrig, 1997; Cayuela *et al.*, 2019), or by manipulating resource characteristics in nature (Kneidel, 1984b) and assessing the outcomes for generalists and specialists alike. We encourage researchers to use ERPs and their communities as models to understand these eco-evolutionary processes – particularly regarding the predictions and questions outlined above.

Importantly, it will take quantifying the spatial and temporal variation of disparate ERP types, among different environmental contexts (e.g. different habitats and seasons), with outcomes for consumer adaptation (e.g. resource \times environment \times genotype interactions), if we are to understand better how the remarkable variability of ERPs shapes the eco-evolutionary dynamics of their communities. As we have highlighted, ERPs are united by distinct characteristics, each of which can be quantified and manipulated. We expect that certain resource types will vary more in specific characteristics than others, for example fungi and puddles are expected to be less variable in spatial predictability throughout landscapes compared to carrion (McLachlan & Ladle, 2001; Fontanarrosa *et al.*, 2009). Although these differences may seem superficial, we have articulated that they are in fact key underlying factors driving the eco-evolutionary dynamics of consumers and are therefore crucial benchmarks for informing theory. For example, different patches of seaweed wrack may vary in their heterogeneity and ephemerality which could directly affect the necrobiome community and its function in different coastal ecosystems. Comparing between resource types, high levels of patchiness of parasitic galls may not produce the same ecological outcomes (metacommunity diversity and abundance) as high levels of patchiness of carrion. This variation within and between resources is also likely to correspond with species-specific adaptive trajectories (Manning *et al.*, 2004; Barton *et al.*, 2013b) and the same highly ephemeral patches of carrion may exert very different selective pressures on their various consumer taxa (i.e. beetles *versus* blowflies).

Importantly, climate change is likely to have profound effects on habitat suitability for many species (Hotta *et al.*, 2019), including the many thousands of species that utilise ERPs. Climate change may be greatly shifting the spatiotemporal patterns of ERPs and altering the variability of resource characteristics such as patchiness, ephemerality variance, and recurrence intervals. It is important that more conservation research is directed towards ERP communities, particularly because ERPs form a major foundation of ecosystems. They will also make good models for understanding the responses of

communities to climate change, as well as the evolutionary responses of individual species to changing environmental conditions. As highlighted many times throughout this review, the highly variable and unpredictable nature of ERPs may correlate with greater phenotypic plasticity in ERP-breeding species. Future research could focus on whether ERP-breeding species have greater adaptive potential compared to non-ERP-breeding species, and whether ERP-breeding species might be better able to adapt to future climate change scenarios.

A final implication of our framework is the powerful potential for ERPs to be useful tools in biodiversity conservation and restoration in land and waterway management. ERPs support a large biodiversity, are often small and (relatively) easily manipulated, and can potentially drive the dynamics of communities in ways that other resources are unable to or take far longer to achieve. Using our framework, researchers can begin to build new predictive models and test how ERPs might be used to solve biodiversity management problems (Stiegler *et al.*, 2020). In some parts of the world, ERPs are already manipulated for conservation, for example by the addition of coarse woody debris (Sandström *et al.*, 2019). Leaving dead timber in the landscape has been repeatedly shown to be important for vertebrates as well as saproxylic insects (Grove, 2002). Management options include fallen *versus* standing timber (Harmon *et al.*, 1986), or spatial proximity and arrangement of logs to allow movement of organisms across landscapes (Barton *et al.*, 2009). Likewise, knowledge of ERPs may be used to manipulate and slow the progress of invasive species (Lutscher & Musgrave, 2017). There are lessons to learn from restoration ecology (Petranka & Holbrook, 2006), and a clear research agenda can be established for other important ERPs such as animal carcasses, aquatic leaf packs, wood debris, and seaweed wrack using similar principles. A goal and challenge for applied ERP research is to identify ways that contrasting ERPs (e.g. carrion *versus* dung *versus* leaf packs) might be managed in ways that enrich landscapes and waterways and their differences exploited to benefit multiple dimensions of biodiversity.

VIII. CONCLUSIONS

(1) The unique dynamics of ERPs have long been appreciated, but there has been no attempt to articulate their shared spatiotemporal characteristics or to synthesise their ecological and evolutionary influences on consumers. This has left us with no way to distinguish ERPs clearly from other resources, or to appreciate how they have shaped organisms, communities, and ecosystems.

(2) We clarify that ERPs are any distinct consumable resource which (i) is homogeneous (genetically, chemically, or structurally) relative to the surrounding matrix, (ii) hosts a discrete multitrophic community assemblage with species that cannot replicate solely in any of the surrounding matrix, and (iii) cannot maintain a balance between depletion and renewal, which in turn prevents the resource from supporting

multiple generations of consumers or reaching a community equilibrium.

(3) We describe the spatiotemporal characteristics that unite ERPs and show how variation in these parameters can shape communities and eco-evolutionary processes. This is captured in a new unifying framework, which highlights why differences within and among ERPs are important and demonstrates their crucial role in shaping species adaptations and community diversity throughout patches and landscapes.

(4) The future of ERP research should focus on elucidating precisely how inter- and intra-resource variation occurs in nature – with a particular focus on resource \times environment \times genotype interactions. This knowledge will be crucial for the parameterisation of ecological models, the quantification of adaptive trajectories, and for understanding the remarkably unique eco-evolutionary dynamics of these ubiquitous resources.

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