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REVIEW PAPER

Persistence through tough times: fixed and shifting refuges in threatened species conservation

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Abstract

It may be possible to avert threatened species declines by protecting refuges that promote species persistence during times of stress. To do this, we need to know where refuges are located, and when and which management actions are required to preserve, enhance or replicate them. Here we use a niche-based perspective to characterise refuges that are either fixed or shifting in location over ecological time scales (hours to centuries). We synthesise current knowledge of the role of fixed and shifting refuges, using threatened species examples where possible, and examine their relationships with stressors including drought, fire, introduced species, disease, and their interactions. Refuges often provide greater cover, water, food availability or protection from predators than other areas within the same landscapes. In many cases, landscape features provide refuge, but refuges can also arise through dynamic and shifting species interactions (e.g., mesopredator suppression). Elucidating the mechanisms by which species benefit from refuges can help guide the creation of new or artificial refuges. Importantly, we also need to recognise when refuges alone are insufficient to halt the decline of species, and where more intensive conservation intervention may be required. We argue that understanding the role of ecological refuges is an important part of strategies to stem further global biodiversity loss.

Keywords Endangered species · Biodiversity conservation · Fire · Niche · Predators · Press, pulse and ramp stressors

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Introduction

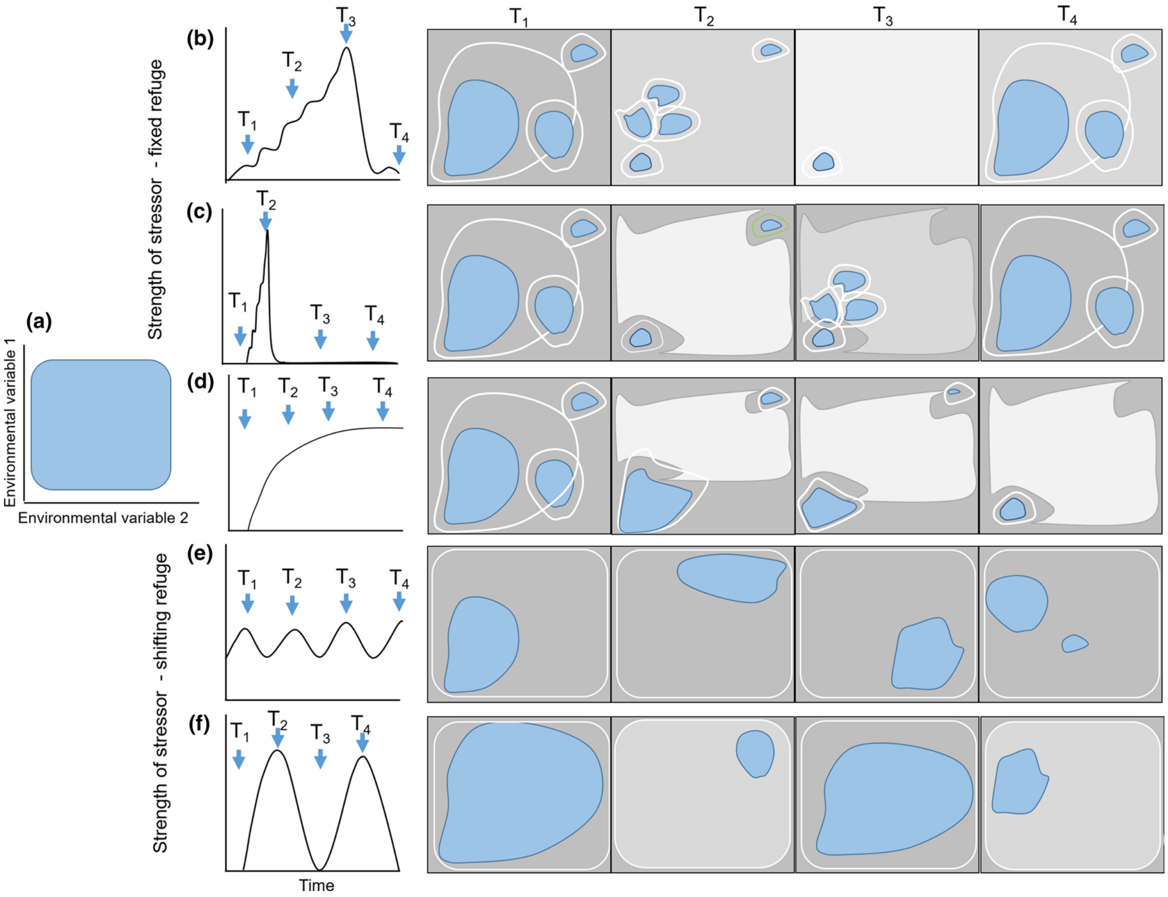
Species extinction rates are currently estimated to be a thousand times above ‘normal’ background rates (De Vos et al. 2014; Woinarski et al. 2015) due to pervasive anthropogenic threats including land-use change and impacts from introduced species (Sala et al. 2000). In the presence of such threats, species may retreat to ecologically-determined refuges, which are areas that reduce the intensity of stressors or provide advantages in biotic interactions (Berryman and Hawkins 2006). When stressors ease, these species may then recolonise surrounding areas. Most research has focussed on refuges that are fixed in space (e.g., Selwood et al. 2015b), but there is increasing recognition of the importance of refuges that shift throughout the landscape (Pavey et al. 2017). It is crucial to locate and protect refuges, because unidentified refuges are at risk of being lost through habitat modification (e.g., development) or inappropriate management (e.g., severe fire). By identifying refuges, they can also be enhanced or created through management.

The aims of this review are to advance the conceptual basis of the ecological refuge by defining and describing fixed and shifting refuges that are relevant to biodiversity conservation, and to clarify the role of ecological refuges in protecting threatened species from stressors. We build upon Keppel et al. (2012) and Pavey et al. (2017) and use the term ‘refuge’ to refer to ecological places that relieve individuals or populations from stressors over ecologically-relevant temporal and spatial scales (Table 1). By contrast, the term ‘refugium’ (plural: refugia) refers to a place that has enabled species to persist at a location over geological time scales (Keppel et al. 2012), such as when climate change has made much of their former distribution unsuitable (Table 1). For example, sites free of glaciation during ice ages, from which species expanded their ranges when the climate warmed, would be considered refugia (Rull 2009). Where populations use such refugia temporarily over ecological time scales, the same place can serve dual functions as both refuge and refugium. By focussing on the ecologically-defined refuge, our definition does not include places such as ‘remnants’ or protected areas such as reserves that are sometimes referred to as ‘refuges’ (e.g., Wildlife Refuge reserves; Keppel and Wardell-Johnson 2012), unless they also fit our definition of an ecological refuge.

We consider refuges in terms of a species’ niche: a hyper-volume in environmental space within which a species’ population can persist (Hutchinson 1957). Holt’s refinement of this concept recognises that organisms may need to move between favourable locations to remain within their niche (Holt 2009). We suggest further that a refuge is a physical place that permits a species to remain within its niche during times of stress, when formerly occupied areas fall outside the species’ tolerances. A niche can be categorised into fundamental and realised volumes (Table 1). The fundamental niche is a larger volume that could be occupied in the absence of deleterious interactions with other species, while the realised niche is the smaller volume occupied in the presence of interspecific interactions such as competition, predation and disease. A population may also contract to refuges if the abiotic environment changes, taking previously habitable areas outside the species’ fundamental niche (e.g., because of a heat wave), or because of a contraction of the realised niche due to change in biotic interactions (e.g., with the introduction of a new predator or superior competitor). Therefore, the refuge is the place where an individual’s or a population’s realised niche persists, despite other parts of the range becoming inhospitable. In some cases, the niche requirements for reproduction may be a subset of the available habitat or refuges (Fig. 1). Species’ susceptibility to stressors and reliance on refuges can also vary across niche space (Scheele et al. 2017). For example, waterfall frogs *Litoria lorica*

Table 1 Glossary of key terms

Term	Definition	References
Refuge (plural refuges)	A physical space that remains within a species' niche during times of stress, which an organism occupies over ecological time frames (days to decades)	Keppel et al. (2012), Pavey et al. (2017)
Refugium (plural refugia)	A physical place that remains within a species' niche, and is large enough to support populations of species over evolutionary time scales (millennia)	Keppel et al. (2012)
Hutchinson's niche	Hyper-volume in environmental space within which a species' population can persist	Hutchinson (1957)
Fundamental niche	The volume of environmental space that a species could occupy in absence of deleterious interactions with other species	Hutchinson (1957)
Realised niche	The subset of the fundamental niche that a species can occupy in the presence of interspecific interactions such as competition, predation and disease	Hutchinson (1957)
Press stressor	A stressor that has a sustained impact. Press stressors can occur sharply, and can increase in intensity through time or be maintained at a constant level. *Sensu* "press perturbation" (Bender et al. 1984) or "press disturbance" (Nimmo et al. 2015)	Bender et al. (1984), Lake (2000), Nimmo et al. (2015)
Pulse stressor	A stressor with a relatively instantaneous occurrence, which is sharply delineated, and eventually relaxes. e.g., floods or fires	Bender et al. (1984), Lake (2000), Nimmo et al. (2015)
Ramp stressor	A stressor that increases in intensity steadily through time, sometimes without an endpoint, or that reaches an asymptote. e.g., drought	Lake (2000), Nimmo et al. (2015)
Fixed refuge	A refuge that remains fixed in space over an organism's lifespan, or longer. A fixed refuge has properties that make it consistently more suitable than the surrounding landscape	Pavey et al. (2017)
Shifting refuge	A refuge that has properties that make it more suitable for an organism than the surrounding landscape for a period of time shorter than an individual's lifespan	Pavey et al. (2017)


(a)
Environmental variable 1
Environmental variable 2
(b)
(c)
(d)
(e)
(f)
Strength of stressor - fixed refuge
Strength of stressor - shifting refuge
T1
T2
T3
T4
Time

◀ **Fig. 1** A niche perspective of ecological refuges. **a** The niche space of a species in relation to two environmental variables. **b** An example of the niche mapped in geographic space over time during a ramp disturbance (e.g., a drought), in addition to the limits of species' mobility (white line). As the stressor builds in intensity through time (**b**, T_1–T_3), the niche space of the species shrinks (**b**, T_2), leading to a loss of overall niche space until the population is confined to a refuge (**b**, T_3). As the ramp disturbance continues to intensity, the population is reduced to a small refuge (**b**, T_3), until the stressor is lifted and recovery occurs (T_4). **c** An example of changes in niche space in relation to a pulse disturbance (e.g., wildfire). T_1 shows the niche space prior to the pulse disturbance. In T_2 the pulse disturbance occurs (light shading), reducing the area with the species niche, leading to the eventual loss of niche space (top right of T_3). As time since the disturbance increases (T_3–T_4), succession allows the persistence niche to expand and eventually return to the pre-disturbance state. **d** An example of changes in niche space in relation to a press disturbance (e.g., introduced predators). As the press disturbance (light shading) builds from T_2 to T_4, the niche space of the species is reduced and eventually isolated areas within the niche are lost (i.e., through extinction debt). Eventually the niche space is confined to a small refuge. The press disturbance is ongoing, and so no recovery occurs. Shifting refuges: **e** species move continuously between patches; exploiting a patch until the resource availability declines before moving to the next patch; **f** species using the landscape, but retracting to refuges in the presence of the stressor. The location of the refuge shifts depending on the conditions

(listed as Critically Endangered under Australia's Environment Protection and Biodiversity Conservation Act 1999) and *L. nannotis* (Endangered) can survive *Batrachochytrium dendrobatidis* infections in sunny sites, but have been extirpated from cooler rainforest sites (Puschendorf et al. 2011).

While most research on the ecological refuge concept has focussed on refuges from a single stressor, such as climate warming (Keppel et al. 2012) or fire (Robinson et al. 2013), many species are affected by multiple, interacting stressors, that can accelerate population declines (Doherty et al. 2015) via additive, dominant, antagonistic or synergistic effects (Côté et al. 2016). In many cases, refuges are likely to protect species from multiple interacting stressors, so understanding the relative contribution of each stressor to species declines can be difficult, and some effects could be masked (Kutt and Fisher 2011). For example, rocky gorges can simultaneously provide animals with refuge from fire (Dobrowski 2011), and buffer them against thermal and hydric stress (Reside et al. 2014) and predation pressure (McDonald et al. 2013). From a management perspective, it is therefore important to understand how individual species use refuges (Magoulick and Kobza 2003). Identifying refuges solely from the absence of single stressors could inaccurately rank their importance.

Refuges have traditionally been viewed as fixed in space; as places with properties that decouple the local conditions from the broader environment (Dobrowski 2011). However, stressors are often spatially dynamic and, therefore, the factors that alleviate or accentuate them can also shift. Shifting refuges are likely to be particularly important in regions of high natural climatic variability, such as arid zones, because these refuges depend on irregular rainfall (Pavey et al. 2017).

We identify refuges as emerging through two mechanisms: patchiness and buffering of stressors. Patchiness refers to the distribution and intensity of the stressor across space. This is particularly apparent with press (persistent stressors, e.g., urbanisation) and pulse (sudden stressors, e.g., floods and fire) stressors (Fig. 1c) (sensu Bender et al. 1984) that result in a mosaic of patches that are affected by stressors to differing degrees. Less affected patches can act as refuges until more severely affected areas recover. For instance, fire refuges can be areas that escape fire, either due to stochastic or deterministic factors (Leonard et al. 2014; Robinson et al. 2013). Buffering refers to areas that are exposed to the disturbance, but have properties that diminish the impact of the stressor on an individual or population. For instance, Robinson et al. (2016) found that gullies in mesic forests maintained greater bird species richness and abundance, and a distinct bird assemblage, compared to adjacent slopes, even when burnt. Burnt gullies also provide refuge for bush rats (*Rattus fuscipes*) in both wet and dry forests (Banks et al. 2011). Buffering is also evident in response to ramp stressors (Fig. 1b) (stressors that build gradually, such as drought; Lake 2000); for example, riparian sites can diminish the impact of severe drought on bird communities (Nimmo et al. 2015).

Where threatening processes have eliminated a species from most of its former distribution, species can be limited to a reduced geographic range, or restricted to islands (Channell and Lomolino 2000; Fisher 2011). In keeping with previous definitions, we focus here on refuges as places from which a species could potentially expand when a stressor is alleviated; we do not consider the entire remaining extent of a species' reduced geographic range (i.e., all remaining habitat) as a refuge. However, we acknowledge that this may not always be a clear distinction, and depends on the timescale in which stressors could be alleviated.

We focus on threatened vertebrates to illustrate the nature and functioning of the various types of refuges in this context, incorporating examples from a diverse range of environments (e.g., arid zone, woodlands, tropical rainforests) and stressors (drought, fire, introduced predators, disease), that are globally relevant (Doherty et al. 2016). Many of our case studies are of Australian species, which may be predisposed to refuge use as a result of exposure to highly variable rainfall regimes (Van Etten 2009) that lead to variable productivity, fire, and pronounced population fluctuations (Greenville et al. 2014). Similar patterns of refuge use are likely to be found in other locations with variable climates and conditions, for example in arid and semi-arid rangelands across the globe (Holmgren et al. 2006; Labbe and Fausch 2000; Milstead et al. 2007; Pavey et al. 2017), and hence conservation approaches developed by our refuge concept are likely to have broad application. While not the main focus of our review, refuges have also been noted as important for plants, particularly refuges that provide relief from herbivory (Beschta 2005) and disease (Puno et al. 2015). Assessments of refuge use by threatened species are rare; therefore, we include some non-threatened species examples that inform hypotheses of refuge use by threatened species.

Fixed refuges

Fixed refuges are those that remain fixed in space over an individual's lifespan, or longer. Fixed refuges can arise through either patchiness or buffering, and are 'coarse-grained' environments in the sense of Levins (1968). These places or structures may act as refuges intermittently, depending on the longevity of the stressors. For instance, riparian corridors might function as climate refuges for woodland birds during prolonged droughts, acting as refuges in only 10 of every 100 years (Bennett et al. 2014a). Alternatively, fixed refuges may be more permanently used where stressors are persistent. For example, native mammals use rocky outcrops in the presence of persistent 'press' stressors (such as introduced predators and herbivores), at least until those stressors are ameliorated (McDonald et al. 2017). However, the permanence of the refuges themselves forms a spectrum from those that are fixed in space over evolutionary or geological time scales (e.g., floodplain ecosystems; Selwood et al. 2016), to those that last for decades (e.g., long unburned vegetation patches; Berry et al. 2015a).

Fixed refuges can be products of topographic complexity, including mountain ranges, rocky gorges, boulder piles, gullies or slopes (McDonald et al. 2015; Reside et al. 2014).

They may also include regions of reliable water such as riparian zones, persistent waterholes, and drainage lines with accessible groundwater (Nimmo et al. 2016; Selwood et al. 2015b). These physical features can support population persistence by protecting individuals from death or reproductive failure through mechanisms including: mediating local climate; buffering against extreme weather events (Dobrowski 2011); creating patchiness in fire by reducing fuel loads and risk (Berry et al. 2015b; Leonard et al. 2014), increasing food and water availability (Dickman et al. 2011), and providing vegetation cover (McDonald et al. 2016). Physical features can also alter competition between species. For example, refuges for the Critically Endangered red-fin blue-eye fish (*Scaturiginichthys vermeilipinnis*) occur where competition with the introduced mosquitofish *Gambusia holbrooki* is reduced. The red-fin blue-eye is endemic to a single complex of Great Artesian Basin springs in the Lake Eyre Basin of central Australia. It currently survives only in refuges where the springs are large and deep enough for active avoidance, and in remote springs where mosquitofish have not yet invaded (Kerezsy and Fensham 2013).

Fixed refuges from fire

Fixed refuges from fire have been documented in a wide range of ecosystems, including forests, heathland and deserts (Berry et al. 2015b; Krawchuk et al. 2016; Leonard et al. 2014; Mackey et al. 2012; Pavey et al. 2017). Fixed fire refuges tend to result from physical barriers that create burn patchiness, allowing species to survive the fire event, persist after the fire, and eventually recolonise the broader landscape (Robinson et al. 2013). They include rocky substrates, gullies, waterways, cliffs, clearings, and other places where vegetation is discontinuous due to landscape heterogeneity (Robinson et al. 2013) (Fig. 1c). Frequently and extensively burnt areas lack structural shelter such as fallen timber, dense understorey vegetation and standing tree hollows, leaving animals exposed and vulnerable to predators (Murphy et al. 2018). Refuges from fire can therefore provide areas that remain within a species' fundamental niche (e.g., for species that cannot thermoregulate in exposed, burnt areas) and realised niche (e.g., by providing protection from predators).

Gullies often escape fire due to their low topographic position and higher moisture content (Leonard et al. 2014). Unburned gullies within wet forests shelter small mammals during and immediately after fire, when survival declines in exposed burnt areas (Swan et al. 2016). Swan et al. (2016) found that the abundance of agile antechinus (*Antechinus agilis*) increased in gullies post-fire, and suggested that individuals shifted into the gullies from the burnt areas (Table 2). In contrast, bush rats declined in burnt areas without a concomitant population increase in gully areas, suggesting that only the pre-fire residents occupied the gullies. Gullies also support higher densities of arboreal mammals such as koalas (*Phascolarctos cinereus*) than adjacent slopes, with populations in gully refuges supplying individuals for recolonization of nearby, more severely burnt areas (Chia et al. 2015). Finally, gullies can protect mature, hollow-bearing trees, such as mountain ash (*Eucalyptus regnans*) that are essential for the Critically Endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) (Lindenmayer et al. 2013).

Similarly, rock outcrops act as barriers for fire, protecting patches of long-unburned heathland which provide fundamental and realised niche space for small populations of threatened mammals and birds (Danks 1997; Stead-Richardson et al. 2010). Unburnt heath in Two Peoples Bay in south-west Western Australia protects the Vulnerable quokka (*Setonix brachyurus*), Critically Endangered Gilbert's potoroo (*Potorous gilbertii*), and threatened birds including the Vulnerable noisy scrub-bird (*Atrichornis clamosus*) (Danks 1997),

Table 2 A summary of refuge types, examples of species that use these refuges, and management options

Stressor	Refuge: species example	Management options	References
Fixed			
Fire	*Gullies* agile antechinus, Leadbeater's possum, koalas *Rock outcrops* central rock-rat *Unburnt heath (protected by rocks)* quokka, Gilbert's potoroo, noisy scrub-bird, western bristlebird, western ground parrot	Protect the gullies and outcrops from fire via strategic hazard-reduction burns in surrounding area	McDonald et al. (2016), Swan et al. (2016)
Drought	*Permanent waterholes* invertebrates, fish *Riparian areas* woodland birds *Drainage channels* night parrot	Protect drainage refuges from livestock. May require predator control Preserve natural hydrological systems Use environmental flows to replenish waterholes that act as refuges during extreme drought	Kerezsy et al. (2013), Mancini (2013), Murphy et al. (2018), Nimmo et al. (2016), Robson et al. (2008)
Predators	*Rock outcrops* northern quoll, golden-backed tree rat, black-footed tree rat, central rock rat *Complex ground cover* quokka	Employ predator abatement methods, e.g. maintain dingo population, predator baiting	Hernandez-Santin et al. (2016). Hohnen et al. (2016), McDonald et al. (2016), McGregor et al. (2015), Pavey et al. (2017)
Disease	*Warmer microclimates* common mistfrog, growling grass frog *Saline aquatic conditions* growling grass frog	Regulate visitors, maintain equipment hygiene Protect warmer and/or more saline wetlands or creeks from development Manipulate existing habitat to reduce suitability for chytrid fungus (e.g. increase temperature via weed removal, increase salinity) Create artificial wetlands with refuge properties	Heard et al. (2015), Roznik et al. (2015)
Shifting			
Fire	*Recently burnt areas near long unburned hummocks* greater bilby, great desert skink, *Long-unburned spinifex* mallee emu-wren, Carpentarian grasswren, night parrot, great desert skink, sandhill dunnart *Ecotone between sclerophyll and rainforest* eastern bristlebird, northern bettong, Hastings River mouse	Prescribed burning to manage extent and spatial arrangement of refuge burnt within each season. Control weeds that alter fire regimes	Baker (1997), Brown et al. (2009), Cadenhead et al. (2016), Moore et al. (2015), Moseby et al. (2016), Perry et al. (2011), Pyke and Read (2002), Southgate and Carthew (2007), Vernes and Pope (2001)

Table 2 (continued)

Stressor	Refuge: species example	Management options	References
Drought	*Run-on areas in arid country* plains mouse *Resources in gidgee woodland* sandy inland mouse *Inland flood pulses* ducks, waders	Preserve natural hydrological systems; preserve/restore relevant native vegetation; Control weeds (i.e., buffel grass) and exclude livestock that alter resources in woodlands	Butler and Fairfax (2008), Dickman et al. (2011), McEvoy et al. (2015), Pavey et al. (2017), Roshier et al. (2006), Roshier et al. (2002)
Predators	*Gastrolobium thickets* numbat, woylie, northern quoll, eastern pebble-mound mouse, southern black-throated finch *Dingo populations* dusky hopping-mouse, yellow-footed rock-wallaby, greater bilby, mallee fowl	Manage fire to maintain thick vegetation; maintain dingo populations	Bateman et al. (2010), GHD (2012), Hopper (1991), Letnic et al. (2012), Short et al. (2005), Vanderduys et al. (2012)

the Vulnerable western bristlebird (*Dasyornis longirostris*) and Critically Endangered western ground parrot (*Pezoporus flaviventris*).

Fixed refuges of permanent water

Permanent waterways, land springs (such as the groundwater-dependent springs of the Great Artesian Basin) and riparian vegetation are important components of many species' niche space and can provide fixed refuges in both arid and mesic regions (Davis et al. 2017). The few deep, persistent waterholes in ephemeral rivers that become isolated during dry periods serve as refuges for dryland species during droughts. In the arid Cooper Creek system in central Australia, 3% of waterholes are able to persist for more than 2 years without additional flows, each supporting unique hydrology, physico-chemical profiles and biotic assemblages (Sheldon et al. 2010). The largest of these waterholes, such as Cullyamurra near Innamincka, are several kilometres long and up to 26 m deep, and provide refuge through extended droughts (Mancini 2013). Once stream flows resume, these waterholes are a source population for many aquatic taxa, including fish (Kerezsy et al. 2013) and macroinvertebrates (Marshall et al. 2006). Irregular flood-pulses enable aquatic species that are otherwise restricted to such refuges to move hundreds of kilometres to channels, lakes and floodplains to reproduce (Kerezsy et al. 2013; Mancini 2013; Robson et al. 2008).

River systems also provide fixed refuges for terrestrial species by maintaining riparian vegetation when surrounding habitat degrades. For example, landscapes with high levels of riparian tree cover were buffered from the effects of the Millennium Drought in southern Australia and retained more woodland bird species (Haslem et al. 2015; Nimmo et al. 2016), which have been nominated for listing as a Threatened Ecological Community (Environment Protection and Biodiversity Conservation Act 1999; Fraser et al. 2019). However, drought protection provided by riparian refuges differed by species, and following this drought only some species recovered to recolonise the surrounding landscape (Bennett et al. 2014b; Selwood et al. 2015a). Similarly, fewer bird species declined in floodplain compared to non-floodplain ecosystems during the same drought period (Selwood et al. 2015b). Over longer time frames, floodplain ecosystems allow some species to persist in arid landscapes from which they would otherwise be absent (Selwood et al. 2016).

Fixed refuges from predators

Fixed refuges from predators are places where the risk of predation is permanently reduced because (1) predators' access to prey is decreased (i.e., the refuge buffers the effects of predation), and/or (2) predator abundance is low due to habitat unsuitability or dispersal barriers that prevent colonisation (i.e., patchiness in the predator distribution). Feral cats (*Felis catus*) and introduced red foxes (*Vulpes vulpes*) are responsible for suppressing populations of many threatened Australian species (Kutt 2012; Moseby et al. 2015), and act as a press stressor (Fig. 1d). However, they can also act as pulse stressors after high rainfall (addressed in shifting refuges section, below). Complex habitats provide refuge by reducing the hunting success of feral cats (McGregor et al. 2015). For example, rock outcrops serve as fixed refuges for the Endangered northern quoll (*Dasyurus hallucatus*), Vulnerable golden-backed tree rat (*Mesembriomys macrurus*), and Endangered black-footed tree rat (*M. gouldii*), because cats occur at low density and are less active in rock outcrops than in non-rocky habitats (Hernandez-Santin et al. 2016; Hohnen et al. 2016; McDonald et al. 2016; McGregor et al. 2015; Pavey et al. 2017). Similarly, refuges for the Critically Endangered central rock-rat (*Zyzomys pedunculatus*) occur on high elevation ridges of the West MacDonnell Ranges in arid central Australia. Central rock-rats need areas with a fire frequency of at least every 5 years to provide early-succession plants for food, but burned areas expose them to predation by feral cats (McDonald et al. 2016; Pavey et al. 2017). Small populations of central rock-rats have persisted where abundant rock crevices provide refuge from cats (McDonald et al. 2015) and outcrops fragment large fires, creating suitable vegetation for foraging adjacent to shelter (Pavey et al. 2017).

More complex and higher ground cover is also associated with the persistence of small mammals in forest, woodland, heathland and grassland habitats (Kutt and Gordon 2012). The Vulnerable quokka in south-western Australia requires dense riparian and long-unburned heathland vegetation for protection from cats and foxes, and young vegetation for grazing, and so only persists where recently burned (< 2 years ago) patches are adjacent to long-unburned (~ 20 years) vegetation (De Tores et al. 2007).

Fixed refuges from disease

Diseases pose serious threats to a range of taxa globally, particularly amphibians which are affected by chytridiomycosis, caused by chytrid fungus (Skerratt et al. 2016); and plant communities, which experience dieback caused by the root-rot fungus (*Phytophthora cinnamomi*) (Cahill et al. 2008). Limiting the spread of a pathogen and quarantining vulnerable host populations is often difficult to achieve. Once established, eradication of pathogens from the environment is rarely feasible (although see Bosch et al. 2015). Areas where environmental conditions restrict pathogen growth and transmission, or disease manifestation and progression, can provide critical refuges for threatened species from disease. For instance, refuges from chytrid occur for the endangered common mistfrog (*Litoria rheocola*) where reduced canopy cover over a stream increases solar radiation and temperatures, resulting in reduced pathogen prevalence (Roznik et al. 2015).

Understanding the relative niches of hosts and pathogens can help identify species and populations most at risk of disease-mediated decline (Nowakowski et al. 2016), and locate potential refuges from disease (Fig. 2). For example, the environmental limitations (i.e., fundamental niche) of chytrid fungus are now being used to identify refuges for amphibian species from chytridiomycosis. Chytrid fungus grows and reproduces at temperatures of 4–25 °C (with 17–25 °C being optimal), but dies at temperatures at or above 30 °C (Piotrowski et al. 2004). Some species with restricted distributions and high degrees of niche overlap with chytrid have shown substantial declines, and are at high risk, such as the Endangered Baw Baw frog (*Philoria frosti*) and Critically endangered southern corroboree frog (*Pseudophryne corroboree*), while others may now be extinct, such as the mountain mistfrog (*Litoria nyakalensis*) and sharp-snouted dayfrog (*Taudactylus acutirostris*) (Skerratt et al. 2016). In contrast, amphibian species that occur across a broader range of environments such as the armoured mist frog (*Litoria lorica*) have disappeared from cool, moist, higher elevation areas but have been able to persist in warmer, drier, lower elevation areas that are suboptimal for chytrid (Puschendorf et al. 2011). Likewise, warm and relatively saline conditions provide refuges for Vulnerable growling grass frogs (*Litoria raniformis*) against this pathogen across urban landscapes (Heard et al. 2015).

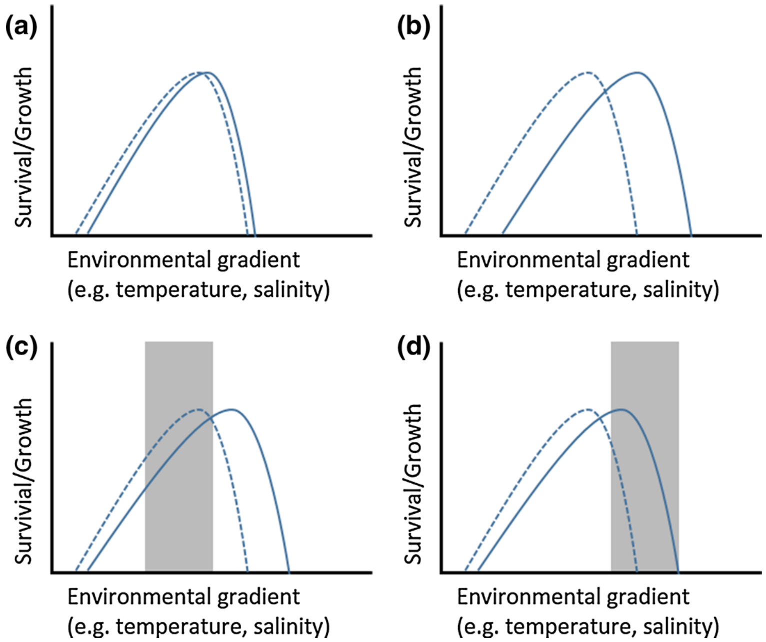


Fig. 2 The degree of niche overlap between hosts (solid line) and pathogens (dotted line) can inform species extinction risk and intervention opportunities: host species with a high degree of overlap with the pathogen niche (**a**) are more at risk than species that can also persist in environments that are unsuitable for the pathogen (**b**). Refuges from disease can be identified by coupling information about niche overlap and microhabitats available to host species (grey shading). Disease impacts are likely to be high at sites where the microhabitats available to hosts are suitable for the pathogen (**c**), in contrast, sites where hosts can exploit microhabitats that are not suitable for the pathogen may act as refuges (**d**). Management actions that shift available microhabitats to favour the host (e.g., **c**→**d**) or enable host populations to establish in refuges can enhance persistence of species threatened by disease

Shifting refuges

Shifting refuges are temporary patches where the availability of food, cover or other essential resources is greater than in the surrounding landscape, allowing individuals or populations to persist where they otherwise would not, at time scales shorter than an individual's lifespan. Thus, the species' niche may remain continuous in the landscape in time but not in space (Fig. 1e, f). Shifting refuges can be truly variable in space, driven primarily by stochastic processes that influence the location of rainfall or fire. Alternatively, the location of a shifting refuge might be partially driven by deterministic factors that are fixed in space, such as landscape features that retain more moisture or are less likely to burn. These partially deterministic shifting refuges sit along the continuum between refuges that are strictly fixed in space, and those that are completely stochastic (Fig. 3). The nature and importance of shifting refuges have been best described in the freshwater context, where refuges that are highly variable in time and space are well-recognised globally as an important phenomenon, supporting freshwater species in times of drought or anthropogenic disturbances that reduce water availability (extensively reviewed in Magoulick and Kobza 2003). For example, refuges for the threatened Arkansas darter (*Etheostoma cragini*) of North America are spatially and temporally dynamic due to intense thunderstorms

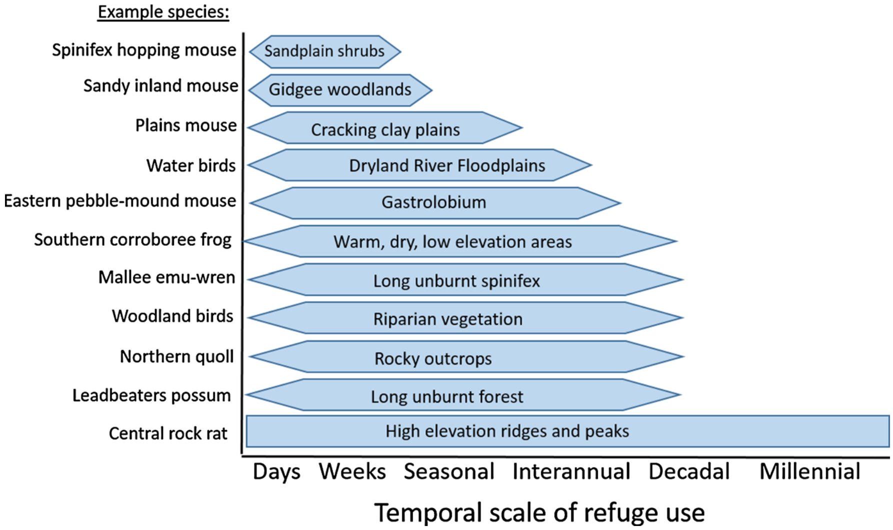


Fig. 3 Examples of refuge types and the species that use them. Refuges can sit along a temporal continuum between shifting and fixed refuges. See text for further detailed discussion on each species

that produce large pools from flash flooding (Labbe and Fausch 2000). These large pools provide refuge from extreme temperatures, hypoxia and predation. In contrast, few studies have explicitly investigated the use of shifting refuges by terrestrial species. In Australia, most evidence for shifting refuges in terrestrial systems comes from the inland arid and semi-arid zones, where fire and water availability play a large part in determining habitat suitability for many species (Newsome and Corbett 1975; Pavey et al. 2017). In particular, rodents in Australia's arid zone are one of the few groups where the use of shifting refuges has been examined in comparative detail.

Shifting refuges arise through stochastic processes and their locations are often unpredictable, forcing dependent species to move at irregular intervals (Newsome and Corbett 1975; Roshier and Reid 2003). Therefore, only mobile species can rely upon shifting refuges (Pavey et al. 2017). However, mobility does not equate to being nomadic, and it does not necessarily require that individuals can make long distance movements. Shifting refuges may only be available for days or weeks, to several years. For example, the spinifex hopping-mouse (*Notomys alexis*), a small murid rodent, exploits refuge patches of tall shrubs on sandplains for periods of 4–5 days before moving long distances through a matrix of inhospitable habitat to reach the next suitable patch (Pavey et al. 2017). The shrub refuges are fixed in position, but the food resources they provide are limited; as animals deplete these resources they are impelled to move on to find new patches where more food is available (Dickman et al. 2011). Although many species expand from fixed refuges once stressors have been alleviated, populations can persist in fixed refuges indefinitely (Fig. 1). In contrast, the location of shifting refuges changes over time; therefore, species that rely on them must either be able to move from one refuge to the next as they become available (Fig. 1e) or recolonise the landscape so that they can capitalise on the refuge as it develops (Fig. 1f).

Shifting refuges from fire

Changes in land use have resulted in dramatically altered fire regimes in many parts of the world (Kasischke and Turetsky 2006; Russell-Smith et al. 2003). In many cases, extensive and intense fires have become more frequent, resulting in large areas of vegetation of similar fire age and a reduction in availability of unburned fire refuges for many species (Burrows et al. 2006; Kasischke and Turetsky 2006; Russell-Smith et al. 2003). Areas that escape frequent or high-intensity burning can be entirely stochastic in their occurrence, resulting from a confluence of processes and events including wind speed and direction, vegetation moisture content, rainfall, disturbance regimes, ignition location, fuel load and fire history (Robinson et al. 2013).

Long-unburnt patches are likely to form refuges for some threatened arid and semi-arid mammals, birds and reptiles, which become more vulnerable to predators, starvation, or exposure when fire removes vegetation cover (Berry et al. 2015c; Davis et al. 2016; Taylor et al. 2012). Mobile predators including birds of prey and feral cats follow the distribution of new fires in these habitats (McGregor et al. 2016; Woinarski et al. 2015), and cats have high hunting success in fire scars in grassland and savanna (Leahy et al. 2016; McGregor et al. 2014). For instance, high-intensity and broad-scale fire exposes the Vulnerable great desert skink (*Liopholis kintorei*) to increased cat predation (Cadenhead et al. 2016; Moore et al. 2015, 2017). However, while exposing species to increasing predation pressure, fire can also create shifting patches of post-fire ephemeral resources that species rely on. For example, the Vulnerable greater bilby (*Macrotis lagotis*) is hunted by cats and foxes, but in parts of its range requires both post-fire ephemeral and fire-sensitive plants for foraging (Southgate and Carthew 2007). The greater bilby is therefore most likely to occur in landscapes that have a high diversity of fire-age classes, including long-unburned grass hummocks for shelter and recently burned areas to forage (Southgate et al. 2007).

Birds that depend on patches of long-unburned spinifex hummock grass for nesting include the Endangered mallee emu-wren (*Stipiturus mallee*), Carpentarian grasswren (*Amytornis dorotheae*) and night parrot (*Pezoporus occidentalis*). These species persist only if refuges of old growth spinifex hummock grassland remain, and spatial shifts in refuges occur at a scale that allow individuals to retreat to these unburned patches when fires occur (Brown et al. 2009; Perry et al. 2011). Likewise, unburnt spinifex grassland is required for population persistence of the great desert skink (Moore et al. 2015) and the sandhill dunnart (*Sminthopsis psammophila*) (Moseby et al. 2016).

The ecotone between sclerophyll (eucalypt) forest and rainforest provides corridors of partly-deterministic shifting refuges from fire for the Critically Endangered northern population of the eastern bristlebird (*Dasyornis brachypterus*) (Fig. 4; Baker 1997). Variation in fire intensity along the damp ecotone results in a shifting distribution of thick tussock-dominated areas that provide critical breeding niche space (Stone et al. 2018). Similarly, fire-moderated wet sclerophyll forest ecotones between rainforest and drier woodland habitat provide refuges for the Endangered northern bettong (*Bettongia tropica*) and Hastings River mouse (*Pseudomys oralis*) (Pyke and Read 2002; Vernes and Pope 2001). For the northern bettong, moister conditions within wet sclerophyll forest provide important hypogeous fungal resources (Abell et al. 2006). Increasingly variable rainfall patterns in this habitat mean that rainforest margins are becoming more important as resource refuges during the dry season, particularly in the bettong's southern range (Bateman et al. 2012).

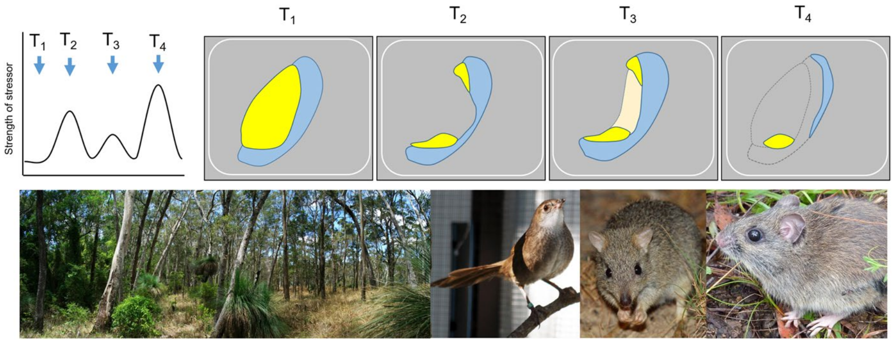


Fig. 4 **a** Shifting ecotone refuges following disturbance. Species occupying ecotonal habitat require intact ecotones for short-term persistence and dispersal between remnant reproductive niche patches (bright yellow) as burnt areas recover (light yellow) following disturbance (T_2–T_3). Increased severity of stressor (e.g., fire) can cause ecotone destruction (T_4) which means species persistence and dispersal is compromised. Shifts in the distribution or quality of an ecotone will depend on disturbance patterns and can be both detrimental (i.e., replacement of reproductive niche with persistence niche) or beneficial (greater availability of post disturbance refuge) to species. **b** Photos from left to right: example of the sharp transitional environment between rainforest and grassy sclerophyll forest occupied by the northern eastern bristlebird; northern eastern bristlebird, northern bettong, Hastings River mouse. (Color figure online)

Shifting refuges from drought

Rainfall is highly variable in space and time in the Australian arid and semi-arid zone (Dean et al. 2009; Van Etten 2009). The availability of moisture is an important determinant of the location of refuges during periods of low rainfall. The Vulnerable plains mouse (*Pseudomys australis*) is an example of a species that uses both fixed and shifting refuges. Plains mouse refuges may be permanently occupied, or occupied for up to 18 months prior to being abandoned (Pavey et al. 2014; Young et al. 2017). Shifting refuges of the plains mouse occur in areas where water accumulates, allowing the shallow-rooted, short-lived grasses and forbs that comprise its diet to germinate in response to the frequent but unpredictable small rainfall (<25 mm) events that occur during long periods of low rainfall (Moseby 2011; Pavey et al. 2016, captured by the niche dynamics in Fig. 1e). High food availability in refuges enables ongoing reproduction and increased survivorship relative to the surrounding landscape, which in turn allows recruitment in the shifting refuges to outstrip mortality (Pavey et al. 2014).

Another small desert rodent that uses shifting refuges is the sandy inland mouse (*Pseudomys hermannsburgensis*, listed as Vulnerable in New South Wales under the Biodiversity Conservation Act 2016). This species occurs in spinifex hummock grassland interspersed with small patches (<0.5 ha to>10 ha) of gidgee woodland (*Acacia georginae*) (Greenville et al. 2009). A long-term study in the Simpson Desert found that small, isolated patches of gidgee woodland act as shifting refuges by providing shelter, food, and lower predation risk compared to surrounding habitat during drought (Dickman et al. 2011). Due to the small size of the individual woodland patches, resources are quickly exhausted—meaning that although the location of individual woodland patches does not change over time, the location of refuges does. The species' ability to exploit these shifting refuges is linked to its broad, omnivorous diet (Murray and Dickman 1994); breeding in response to favourable conditions (Greenville et al. 2016); and ability to move long distances relative to body size (e.g., 14 km over a period of several weeks) (Dickman et al. 1995).

The dryland river systems of the arid interior of Australia support an abundant and diverse wetland-dependent fauna that rely mostly on mobility to exploit temporary wetland resources. In western Queensland and adjacent regions, very large-scale fluctuations in water availability create temporary wetlands through a vast (10^6 ha) interconnected network of channels, waterholes, lakes and floodplains (Bunn et al. 2006b; Roshier et al. 2001; Sheldon et al. 2010). Flood-pulses dramatically increase productivity; for example, one day of algal carbon production at the peak of a flood on the Cooper Creek floodplain (10^3 km) was equivalent to that produced over 80 years in the much smaller permanent waterholes that persist through the dry times (Bunn et al. 2006a). Ducks and waders move to distant flood and rainfall events to breed in a shifting wetland up to half a continent away (McEvoy et al. 2015; Pedler et al. 2014; Roshier et al. 2006). These breeding refuges drive population dynamics at the subcontinental scale (Roshier et al. 2002, illustrated in Fig. 1f).

Partially shifting refuges from predators

Dynamic refuges have long been recognised for their role in predator–prey interactions, resulting from ecological phenomena such as prey and predator densities, crypsis, and mimicry (reviewed in Berryman and Hawkins 2006). Here, we focus on refuges from predation that are spatially dynamic (e.g., shifting), and are important for threatened species conservation.

Mesopredator release can be a severe threat particularly where introduced predators impact native species. This was the case for the Vulnerable Cook's petrel (*Pterodroma cookii*; listed as Vulnerable on IUCN Redlist), a small burrowing seabird threatened by introduced rats and cats on its breeding island in New Zealand. Control of cats resulted in reduced breeding success of Cook's petrel through increases in rat predation, but only at high elevation sites (Rayner et al. 2007).

The presence of a top predator such as the dingo (*Canis dingo*) is important for providing shifting refuges to threatened small mammals, birds and reptiles depredated by cats and foxes (Brook et al. 2012; Johnson et al. 2007; Letnic et al. 2012). Ground-dwelling, medium-sized marsupials show greater persistence where they overlap with dingoes (Johnson et al. 2007), and Vulnerable species including dusky hopping-mouse (*Notomys fuscus*), Malleefowl (*Leipoa ocellata*), yellow-footed rock-wallaby (*Petrogale xanthopus*), kowari (*Dasyuroides byrnei*) and greater bilby are more abundant where dingoes are present (Letnic et al. 2012). These species are all negatively associated with the abundance of foxes. Brook et al. (2012) showed that in areas where dingoes were more active, cats were less active or shifted their activity to avoid times of peak dingo activity. Where dingoes were less active due to lethal control by managers, cat activity was higher and cats were more active earlier in the night (peaking around dusk), potentially enhancing their success in hunting nocturnal small mammalian and reptilian prey. Therefore, refuges created by mesopredator suppression can be spatially and temporally dynamic, and occur on very short time-scales (e.g., hours). Vegetation cover can also be greater in the presence of dingoes, presumably through their suppression of large grazing macropods and herbivores such as goats (*Capra hircus*); this increased cover may also protect small mammals from predators (Wallach et al. 2010).

An added dimension to trophic interactions and their effects on refuges is that disturbance events (e.g., fire) could mediate apex predator control of mesopredators through changes to habitat structure and use. Geary et al. (2018) found that dingoes preferred recently burned areas, and although foxes were not affected by fire history directly, a negative interaction between dingoes and foxes meant that fire had the capacity to indirectly affect fox habitat use as mediated through dingoes.

Other features that provide refuge from predation through increased habitat complexity and cover can be considered partly shifting refuges in the timeframes considered here. For example, shrubs in the genus *Gastrolobium* ('poison pea') can provide refuge for species by forming dense thickets, and providing food through mass seed set (Chandler et al. 2002; Short et al. 2005). Furthermore, *Gastrolobium* spp. contain high levels of fluoroacetate (the poison '1080'), which is more poisonous to introduced species in Australia than to many native granivores and herbivores (Peacock et al. 2011). Consequently, *Gastrolobium* presence is also often associated with reduced stock grazing pressure, resulting in dense ground cover and reduced predation risk from cats and foxes. Furthermore, cats and foxes are poisoned when they eat native prey with elevated levels of the toxin. In south-west Western Australia, the persistence of threatened marsupials including the Vulnerable numbat (*Myrmecobius fasciatus*) and Endangered woylie (*Bettongia penicillata*) is associated with dense stands of *Gastrolobium* spp. (Hopper 1991; Short et al. 2005). In Queensland, *G. grandiflorum* occurs where the Endangered northern quoll and the eastern pebble-mound mouse (*Pseudomys patrius*) (Bateman et al. 2010; Vanderduys et al. 2012) and Endangered granivorous birds such as the southern black-throated finch (*Peophila cincta cincta*) (GHD 2012, 2013; Reside et al. 2019a) persist. Patches of *Gastrolobium* spp. thus provide shifting or partially deterministic refuges for species that are threatened by cats and foxes (Read et al. 2016).

Locating and managing refuges

There is still much to understand of how Australian fauna persist across the landscape through variable conditions, particularly extremes of rainfall, and disturbance events such as fire. Our knowledge is further limited when elucidating the repercussions of changes in anthropogenic land management on the persistence of many threatened species, and the full extent of the role of ecological refuges. Against this background of uncertainty, identifying ecological-scale refuges for threatened species across an extensive landscape is a daunting task. However, particular landscape features such as rocks, gorges and places of water accumulation which provide refuge properties can be found readily through topographical mapping and remotely sensed data. Shifting refuges can be more difficult to locate, but identifying topographic features within a species' distribution, or where apex predator populations exist (e.g., areas free of dingo control) can be useful for narrowing the search. Fine resolution digital elevation models can be used to find cooler aspects (e.g., south-facing slopes) and for locating topographically complex areas, for example by calculating the Topographic Position Index to find valleys (Jenness 2006; Reside et al. 2019b). The availability of high resolution or frequency remote sensing data has greatly enhanced our ability to locate refuges. For example, remote sensed data, such as time series of normalised-difference vegetation index (NDVI) data from the NASA MODIS satellite imagery (Paget and King 2008), have been used to determine the frequency of inundation of temporary wetlands and thereby identify those that are most persistent in an arid landscape

(Roshier et al. 2001). Additionally, remotely-sensed measures of productivity, such as the intercepted fraction of photosynthetically active radiation (fPAR) derived from NDVI, can assist in locating refuges from drought and fire (Haire et al. 2017; Mackey et al. 2012) as they emerge. Light detection and ranging (lidar) technology can provide high definition, three dimensional data on habitat structure, and is increasingly used for studying wildlife-habitat relationships, with great potential for studies of refuges (Vierling et al. 2008). Identification of refuges requires use of species-specific niche criteria (Magoulick and Kobza 2003), and verification of species occupancy through field sampling, particularly during the presence of the stressor (e.g., during drought or after a fire) (Pavey et al. 2017).

Predicting the location of refuges that will persist into the future with changing climate adds substantial complexity and uncertainty, but these refuges are likely to be highly important in the short term, while also serving as long-term refugia. Much attention has been paid to finding and predicting climate change micro-refugia from heat (Keppel et al. 2012), but climate change refugia that provide greater water availability are also crucial (McLaughlin et al. 2017). In many cases, tools used for locating future refugia and current refuges are similar, as many future refugia are identified through areas already providing protective conditions (Reside et al. 2014).

Mapping or identifying sites that act as refuges can help managers to prioritize conservation actions, such as by targeting the management of stressors. For example, exclusion of livestock can enhance the refuge capacity of riparian zones and waterholes for native species during drought (Table 2). Known refuges also could be targeted for management of emerging stressors. For instance, where patches of gidgee woodland provide refuge for small mammals (Dickman et al. 2011), management should be vigilant to combat potential invasions of buffel grass (*Cenchrus ciliaris*), which increases fire intensity, over time destroying gidgee patches (Butler and Fairfax 2008). Likewise, buffel grass invasion into long unburnt spinifex patches that are habitat for the Endangered night parrot is an emerging threat to this refuge, and needs to be a target for management (Murphy et al. 2018).

Identifying refuges can also help ensure that they are protected and not impacted by other threats. Certain types of refuge are likely to be well-represented within protected area networks—for example, disproportionately large areas of steep, high elevation sites, which act as refuges against climate change, are set aside for conservation purposes (Pressey et al. 1996; Scott et al. 2001). In contrast, other refuges, particularly those that occur on highly productive soils or land with development potential (e.g., urban fringes) may have little protection (Venter et al. 2018). For example, old quarry pits act as important disease refuges for the threatened growling grass frog (Heard et al. 2015), but these are gradually being filled in. Incorporating shifting refuges into protected areas and management plans is more complex, because these are not fixed in space. However, broad scale management actions (e.g., protection of top predators and vegetation in reserves) may promote shifting refuges throughout the landscape—with the exact location of these driven by more dynamic processes (e.g., predator movement, fire). A better understanding of the role of refuges could help select areas for protection that best promote the long-term survival of species (Margules and Pressey 2000).

By our definition, refuges are places that are used by species until a stressor is alleviated, after which the species can recolonise the surrounding landscape, and potentially other discrete locations further afield. Consequently, in many cases, a refuge must have appropriate connectivity to suitable habitat to facilitate long-term species persistence. As per standard landscape conservation principles, maintaining or enhancing connectivity between refuges, and between refuges and non-refuge habitat, is therefore an important consideration for management, such as through habitat restoration or maintenance of environmental flows

(Magoulick and Kobza 2003). Furthermore, larger refuges can be more likely to promote population persistence; therefore, management could be focused on larger refuges, or increasing the size of refuges, as in, for example, promoting larger unburnt patches.

After locating refuges in the landscape, and identifying key management actions, the next goal is to identify when refuges are most needed, so that managers can intensify conservation actions in specific refuges for threatened species at critical times. This is particularly crucial for shifting refuges, which may require management only during the period when the area is serving as a refuge. For example, predator management and protection of long-unburned local vegetation are likely to be crucial at the end of periods of high rainfall in arid regions, because introduced predators will have increased during the boom period, and will target threatened native prey as they decline due to decreasing rainfall (Greenville et al. 2014; Letnic and Dickman 2006). Timing is particularly critical in the context of fire management. In particular, managers need to avoid burning fire refuge areas at a frequency that prevents old growth vegetation from developing (Table 2). Additional ‘clean up’ burns after fires can invade gullies, degrade important habitats that otherwise protect species from the immediate effects of fire, and expose species to predators while vegetation in adjacent, more open areas is regenerating (Marlow et al. 2015).

The final key goal for management is to identify when managing existing ecological refuges is insufficient to halt the decline of a threatened species, such as when a threshold of stressor intensity has been crossed, or if no refuges remain for the species. For example, some bird species which contracted to riparian areas were unable to recover after the breaking of an exceptional long dry period, the Millennium Drought (Nimmo et al. 2016). When managing natural ecological refuges is insufficient, understanding the mechanisms that create these refuges can still be a useful strategy to inform management options. For threatened amphibians, knowledge of the fundamental niche of chytrid fungus (e.g., temperature, humidity, pH and salinity tolerances) presents opportunities to reduce habitat suitability for the pathogen, while ensuring the habitat remains suitable for hosts. For example, extinction risk can be reduced for Vulnerable growling grass frogs and potentially green and golden bell frogs (*Litoria aurea*) if refuges from disease are created by constructing warm or saline wetlands (Heard et al. 2015; Stockwell et al. 2014). Translocations outside the species’ natural range or to unoccupied areas of metapopulations may also be a viable solution, if susceptible amphibians are restricted to areas of high pathogen suitability and refuges from disease can be identified (Scheele et al. 2014).

Natural refuges can be successfully mirrored by the construction of fenced enclosures for species vulnerable to introduced predators (Moseby et al. 2009), and creating artificial physical refuges (e.g., by placing boulder piles, nest boxes or constructed hollows into areas that have lost or are devoid of cover, such as recently burnt areas). Artificial refuges, such as recently-constructed in situ artificial springs free of predatory mosquitofish, are important for the conservation of the Critically Endangered red-fin blue-eye fish (Dr Pippa Kern, pers. comm.). Intensively-managed fenced enclosures have often been spectacularly successful in the recovery of target threatened species, although the financial, logistical and ecological maintenance of such projects means they are typically unlikely to be sustainable across evolutionary time frames or at very large geographic scales (Hayward et al. 2014; Moseby et al. 2011). Other examples of intensive management options include translocating threatened species to disease-free areas (e.g., armored mist frog), or to predator-free islands (e.g., Gilbert’s potoroo, kakapo), which has been a successful strategy for the persistence of many threatened species in Australia and New Zealand (Abbott 2000; Ostendorf et al. 2016; Russell et al. 2015). Careful management and monitoring are required to ensure these refuges do not become predator traps, which could be the case for vulnerable species confined to islands or fenced enclosures (Woinarski et al. 2011).

Conclusions

This review highlights recurrent themes on the properties of fixed and shifting refuges, and their interaction with species' realised niches. The major stressors we focus on include predation, changed fire regimes and prolonged drought. Therefore, refuges notably provide:

(1) Cover, in the form of vegetative ground cover, higher-story vegetation complexity, or rocks. Cover typically occurs in areas that are protected from fire, have greater moisture availability, or are protected from grazing. These areas include riparian areas, drainage lines, rocky areas, gullies, areas of toxic or unpalatable vegetation (e.g., *Gastrolobium* spp.), and thickets of fire-responsive species. Cover provides protection from predators, and in some cases increases food supply or provides a suitable microclimate.
(2) Greater availability of water: important habitats include dryland floodplains in addition to riparian areas, drainage lines and rocky areas, as discussed above.
(3) Greater availability of food, as a result of greater water availability, or because of appropriate fire regimes.
(4) Protection from introduced predators through other mechanisms, such as biochemical refuges created by toxic plants or active suppression of problematic mesopredators by apex predators (e.g., dingoes).

For some species, refuges may also provide protection from disease or pathogenic organisms.

Identifying, maintaining, enhancing, protecting and possibly even creating new refuges based on these natural processes are likely to be cost-effective strategies for conserving threatened species. Effective refuges are those that enable species to persist even in the presence of multiple interacting stressors; for example, a combination of altered fire regimes, introduced predators, drought and loss of cover. Understanding the impact of stressors and the efficacy of refuges in maintaining the fundamental and realised niches of threatened species can help inform management, particularly as some stressors have a greater likelihood of being mitigated successfully by management than others. The concepts reviewed here are also likely to be important for species conservation across the globe. If we are to stem the decline of biodiversity, we need to develop a deeper and more integrated understanding of the refuge requirements of species, the stressors that the refuges protect against, the temporal and spatial patterns of refuge availability and use, and how to better protect, maintain and, where necessary, replicate ecological refuges.

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