

## OPINION

# Dynamic management needs for long-lived, sporadically recruiting plant species in human-dominated landscapes

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## Societal Impact Statement

Long-lived, iconic plant species like the baobab, welwitschia, the saguaro cactus or the dragon's blood tree are perceived to be everlasting landscape features due to their pronounced longevity. However, these species are exceptional because new reproductive generations of these plants are infrequently incorporated into existing populations. A strong mismatch exists between the timescale at which these species provide services to society and ecosystems, and the timescale at which their reproductive stages and population development occurs. Here, we draw attention to these mismatches and their relevance for nature conservation and restoration. We argue that more dynamic management programs are necessary to preserve these iconic species for future generations.

## Summary

Plants inhabiting variable environments have to adapt their physiology or demography to maintain fitness and, thus, long-term population viability. Demographic storage through long-lived seeds, juveniles, or adults help to overcome periods where unfavorable environmental conditions preclude successful recruitment into reproductive stages. Such storage components can foster long-term population viability of sporadic recruiters, defined here as species with infrequent recruitment caused by a sporadic release from otherwise prevailing resource limitation. However, the beneficial effect of environmental variation reaches a limit when the species' physiological limits are exceeded or the demographic storage components are not sufficient to overcome periods of unfavorable environmental conditions. This can threaten species' long-term population viability in an increasingly variable, human-dominated world. At the same time, long-lived, sporadically recruiting species provide numerous cultural, socio-economic, and ecological services by being part of local myths and beliefs, or by providing habitat, food, wood, fiber, cosmetic, or medical products. In this contribution, we seek to raise awareness of what we call the 'syndrome of long-lived sporadic recruiters' and the relevance of this syndrome for nature conservation and restoration. We outline key demographic features and highlight the main environmental threats for these plants, exemplified for a set of globally distributed charismatic plant species. We propose that

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fostering the long-term population viability of long-lived, sporadically recruiting plants will require the adaptive implementation of a dynamic management scheme where management actions, monitoring objectives, public outreach and research on the key demographic features of the species are coordinated.

#### KEYWORDS

climatic predictability, disequilibrium, disturbance, ecological memory, extinction debts, historical legacies, longevity, pulse event recruitment

## 1 | INTRODUCTION

Landscapes are defined by geomorphological structures such as mountain ranges, valleys or floodplains. However, plants with striking visual appearance can also be defining elements of landscapes (examples in Figure 1). Although often perceived to be persistent landscape features due to their longevity and size, we argue that an important characteristic of such species are that they recruit, that is, add new individuals to populations, infrequently. Thus, such species should be considered to be rather exceptional components of ecosystems from a demographic point-of-view. In this article, we define recruitment in a strict demographic sense as the establishment of a new generation of reproductive individuals. In other words, recruitment is the outcome of the reproductive effort of current generations and survival through juvenile stages (i.e., recruitment into reproductive size classes), and can be the outcome of both sexual and clonal reproduction.

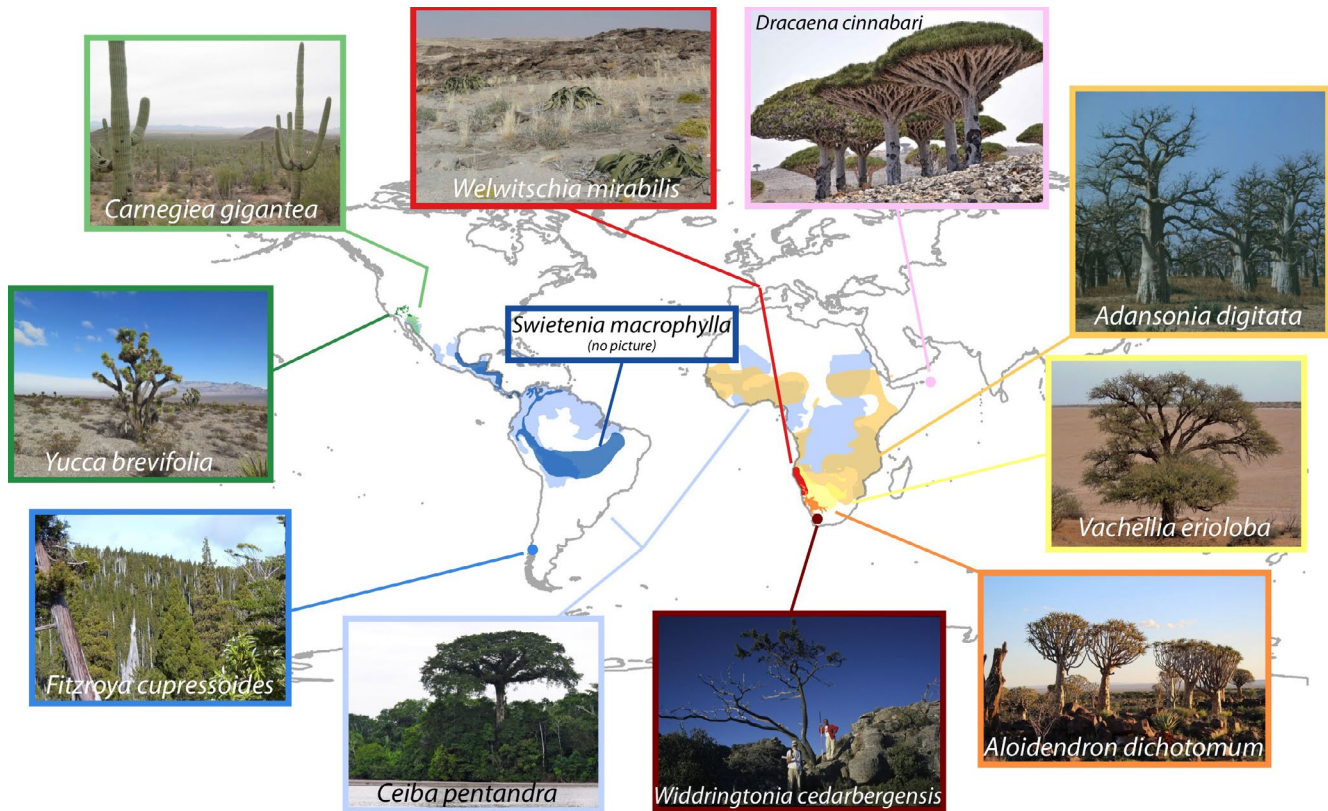
What we observe and presume to be a reflection of current environmental conditions and ecological processes acting on such species might in fact be the remnants of demographic processes and events that occurred decades, or even centuries, ago (cf. Pierson & Turner, 1998). At the same time, many of these iconic, long-lived plant species provide important economic and socio-cultural services beneficial for human society and often serve as keystone species for other species and ecosystem functioning (sensu Paine, 1969). These species are often integral to local myths and beliefs, or provide construction and fire wood, fiber, food, cosmetic, and medical products with local to global economic importance and represent living symbols of entire regions, states, or even countries (see Table 1). However, a strong mismatch exists between the temporal scale at which such long-lived species provide services to society and ecosystems and the timescale at which their recruitment and population dynamics happen. These mismatches should be considered in the context of species and landscape conservation and restoration. However, current conservation and restoration schemes rarely take such temporally discontinuous demographic dynamics into account, which puts these seemingly everlasting species at risk.

The objective of this article is to raise awareness of these demographic dynamics and their relevance to nature conservation and restoration practice. We describe the phenomenon of sporadic

recruitment by outlining common ecological and demographic characteristics of sporadically recruiting species. We use the term the 'syndrome of long-lived sporadic recruiters' to summarize demographic traits (i.e., longevity and infrequent recruitment) that together are characteristic of the species we are referring to in this article. A second objective of this work is to highlight cases where sporadic recruitment in combination with demographic storage components become relevant for nature and landscape conservation and restoration in our increasingly human-dominated landscapes. We exemplify this for a set of iconic plant species with striking visual appearance and high cultural importance (Figure 1). Many more species with variable lifespans including numerous plant species of ephemeral desert vegetation and wetlands as well as many tree species in genera such as *Populus* and *Salix* occurring in disturbance-driven forest ecosystems of the mid-latitudes store reproductive potential over generations and recruit infrequently. However, these species and many other early-successional and disturbance-dependent species are rather short-lived and, thus, would not be classified to be characteristic for the syndrome of long-lived sporadic recruiters discussed in this article. Several other, long-lived, infrequently recruiting species including even common temperate tree crops like Douglas fir (*Pseudotsuga menziesii*) fit with the described syndrome. Rather than an exhaustive overview, the objective on this contribution is to stimulate targeted research on the key demographic features which will be outlined in the following section. Such information is a prerequisite to efficiently account for pronounced disequilibrium conditions in species demographic dynamics but is lacking even for the set of iconic species listed in this paper. In conclusion, we derive recommendations about conservation and restoration strategies to ensure a sustainable maintenance of long-lived sporadic recruiters (species with pronounced sporadic recruitment and strong demographic storage) and the important ecological, economic, and socio-cultural services which are often linked to such species.

## 2 | THE SYNDROME OF LONG-LIVED SPORADIC RECRUITERS

Infrequent, sporadically abundant recruitment—in many cases linked to rare environmental conditions—in combination with



**FIGURE 1** Iconic examples of long-lived sporadic recruiters characterizing entire landscapes. The depicted species occur in the deserts of North America (*Carnegiea gigantea* and *Yucca brevifolia*), temperate South America (*Fitzroya cupressoides*) as well as tropical and subtropical South America and Africa (*Adansonia digitata*, *Aloidendron dichotomum*, *Ceiba pentandra*, *Welwitschia mirabilis*, *Swietenia macrophylla*, *Widdringtonia cedarbergensis*, and *Vachellia erioloba*) and Socotra (*Dracaena cinnabari*). The distribution ranges of the different species are depicted in different colors, which correspond to the colors used in Figure 3. Distribution of the rarest species (*F. cupressoides*, *W. cedarbergensis*, and *D. cinnabari*) are represented as points for the sake of clarity. Distribution ranges were taken from Urrutia-Jalabert, Rossi, Deslauriers, Malhi, and Lara (2015) for *F. cupressoides*, Little (1976) for *Y. brevifolia* and *C. gigantea*, Thomas Schoch (wikipedia.org, CC-BY-SA-3.0.) for *W. mirabilis*, Maděra et al. (2019) for *D. cinnabari*, Pock Tsy et al. (2009) for *A. digitata*, Barnes, Fagg, and Milton (1997) for *V. erioloba*, Jack, Hoffman, Rohde, and Durbach (2016) for *A. dichotomum*, Manders (1986) for *W. cedarbergensis*, Phys.org (2007) for *C. pentandra* and Martinez, Blundell, Gullison, and Grogan (2008) for *S. macrophylla*. Photo credit: Marianne Lauerer (*A. dichotoma*), Klaus Müller-Hohenstein (*A. digitata*), Elisabeth Ofner (*W. mirabilis*), Neelix (*V. erioloba*, public domain from wikipedia.org), Rod Waddington (*D. cinnabari*, CC BY-NC 2.0 from flickr.com), Patricio Novoa Quezada (*F. cupressoides*, CC BY-NC 2.0 from flickr.com) and Vince Smith (*C. pentandra*, CC-BY 2.0 from flickr.com)

pronounced longevity are the defining features of the syndrome of long-lived sporadic recruiters (Figure 2). Pronounced longevity is defined as lifespans of several hundred to several thousand years (see Table 1 for examples). The definition of what 'infrequent recruitment' means varies with longevity and other demographic storage components (e.g., seed and/or sapling bank longevity), but typically results in recruitment intervals of between 15 and 150 years (see Table 1). Low recruitment rates under adverse environmental conditions are caused by high mortality in early life stages, either due to high seed or high seedling mortality but could in principle also happen at later juvenile stages. Seed predation and microbial infection are often typical causes of high seed mortality (Gullison, Panfil, Strouse, & Hubbell, 1996; Vander Wall, Esque, Haines, Garnett, & Waitman, 2006; Whitaker, Pammenter, & Berjak, 2008). High seedling mortality can be induced by, for example, high temporal stochasticity in water availability, which strongly limits recruitment with mortality rates reaching 100%

in extreme cases (Attorre et al., 2007; Barnes, 2001; Venter & Witkowski, 2013).

Infrequent recruitment is often reported in sink populations at species range margins where environmental conditions become increasingly unfavorable for juvenile plants (Parker, 1989 and references therein; Guo, Taper, Schoenberger, & Brandle, 2005). However, for many plant species sporadic recruitment operates throughout the entire range of the species (see e.g., species summarized in Table 1). Generally, sporadically occurring recruitment seems to be a common demographic feature in water-limited environments such as dry savannas or rangelands. In these environments, infrequent, successful recruitment of annuals, perennial herbaceous species, and woody long-lived species is often linked to exceptional rainfall sequences (e.g., Bowers, Webb, & Rondeau, 2009; Goldberg & Turner, 1986).

For woody, long-lived species sporadic recruitment often results in clearly recognizable, even-aged stands of trees (Seymour, 2008 and references therein; Maděra et al., 2019). Nevertheless, this

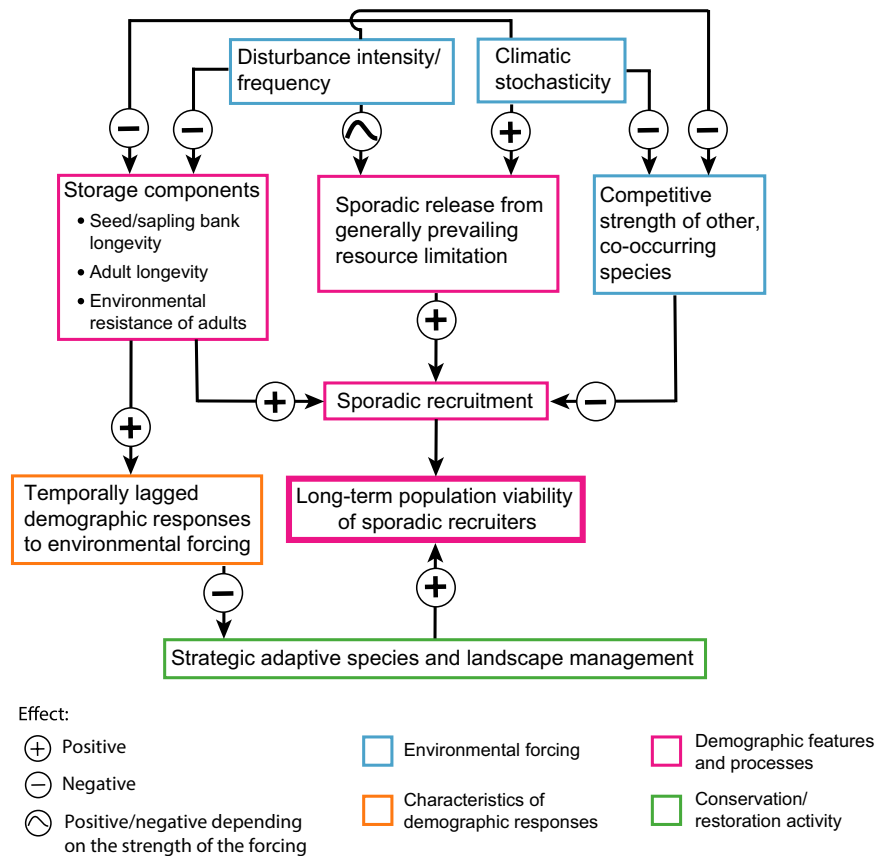
**TABLE 1** Iconic examples of sporadic recruiters with pronounced demographic storage (long-lived sporadic recruiters), their demographic characteristics and ecological, cultural, sociopolitical, and economic importance. Literature references for the listed information are given for each species; information on individual seed weight was taken from the Kew Royal Botanical Gardens Seed Information Database (<http://data.kew.org/sid>)

Common name	Scientific name	Family	Biome	Dispersal mode	Individual seed weight (mg)	Max. life span (yrs)	Recruitment intervals (yrs)	Time to maturity (yrs)	Proximal causes of low recruitment	Drivers of episodic recruitment	Ecological importance	Cultural, sociopolitical and economic importance	References
Baobab	<i>Adansonia digitata</i>	Malvaceae	Savanna	Animals/humans	464.0	1,200	100–150	23	Seedling mortality	Favorable weather conditions	Food, water and habitat for numerous animals	Integral part of numerous local myths and beliefs; used for more than 300 purposes including wood, fiber, food and lifestyle products with regional to global economic importance	(Dhillon & Gustad, 2004; Patrut et al., 2007; Venter & Witkowski, 2010; Sanchez et al., 2011)
Welwitschia	<i>Welwitschia mirabilis</i>	Welwitschiaceae	Desert	Wind	69.0	2,000–3,000	unknown	12–50	Seed/Seedling mortality	Favorable weather conditions	Food and shelter for birds, mammals, reptiles, insects and spiders	Part of the coat of arms of Namibia; Integral part of numerous legends and myths and as being commonly used as economic brand	(Borrmann, 1978; Henschel & Seely, 2000; Henschel, 2012; Pfadenhauer & Klötzli, 2015; Whitaker et al., 2008)
Quiver tree	<i>Aloe dichotoma</i>	Xanthorrhoeaceae	Xeric shrubland	Wind	5.8	350	>15	20–40	unknown	Favorable weather conditions	Food and shelter for birds and other animals	Iconic species of southwestern part of South Africa and Namibia	(Kaleme, 2003; Midgley, Desmot, Esler, & Rundel, 1996)
Cianwilliam cedar	<i>Widdingtonia cedarbergensis</i>	Cupressaceae	Xeric shrubland	Animals	68.0	400	100	40	Seedling mortality	Favorable weather conditions, frequency and timing of fires	unknown	Timber of high importance in historic times (furniture, shipbuilding, fence and telegraph poles), nowadays highly endangered, iconic species of the Western Cape Province, South Africa, high importance for environmental education	(Notten, 2003; White et al., 2016)
Camelthorn	<i>Vachellia erioboba</i>	Fabaceae	Xeric shrubland and savanna	Animals	288.3	240–300	10–20	20	Seed/Seedling mortality	Favorable weather conditions, release from competition with grasses by grazing	Keystone species with many species and ecosystem processes dependent on it	Wood for lumber, fuel and cooking purposes; pods to make a hot coffee-like drink or porridge; highly nutritional fodder for cattle; edible and medicinal gum and bark	(Midgley & Bond, 2001; Seymour, 2008; Steenkamp, Vogel, Fuls, Rooyen, & Rooyen, 2008)
Dragon's blood tree	<i>Dracaena cinnabari</i>	Asparagaceae	Xeric shrubland	Animals	68.0	700	Currently no natural recruitment	>150	Seedling mortality	Favorable weather conditions	Dracaena woodlands are considered as one of the oldest forest communities on Earth	Key endemic species and dominant flagship tree shaping the landscape character of Socotra Island; Local people use it to cure gastric sores, to dye wool, glue and decorate pottery and houses	(Addit & Pavlis, 2004; Adolt et al., 2013; Madêra et al., 2019)
Saguaro	<i>Carnegiea gigantea</i>	Cactaceae	Desert	Water/animals	1.3	300	75–100	30–45	Seedling mortality	Favorable weather conditions (i.e. linked to global volcanic activity or El Niño events)	Nesting habitat, shelter, food for birds and other animals	Fruits of cultural importance for indigenous people, (icon of the Sonoran Desert and the State of Arizona)	(Drezner & Bailing, 2002; Pierson & Turner, 1998)

Continues

TABLE 1 Continued

Common name	Scientific name	Family	Blome	Dispersal mode	Individual seed weight (mg)	Max. life span (yrs)	Recruitment intervals (yrs)	Time to maturity (yrs)	Proximal causes of low recruitment	Drivers of episodic recruitment	Ecological importance	Cultural, sociopolitical and economic importance	References
Joshua tree	<i>Yucca brevifolia</i>	Asparagaceae	Desert	Animals	92.0	1,000	unknown	60	Seed mortality	Favorable weather conditions	Main food resource for insects (Yucca moth) and rodents especially during mast seeding years	Symbol of the Mojave Desert	(Borchert & DeFalco, 2016; Little, 1950; Vander Wall et al., 2006)
Broad-leaf mahogany	<i>Swietenia macrophylla</i>	Meliaceae	Tropical rain forest	Wind	566.0	>180	unknown	10–15	Seed mortality	Disturbance (flooding) creating canopy gaps	Habitat and food for epiphytes and arthropods	Timber of high economic importance; Medicinal plant throughout the Caribbean, threatened by overexploitation, protected in natural range, timber production in South-East Asia	(Brown, Jennings, & Clements, 2003; Gullison et al., 1996)
Kapok	<i>Ceiba pentandra</i>	Malvaceae	Tropical rain forest and savanna	Wind	59.0	500	unknown	unknown	unknown	Disturbance creating large canopy gaps	Habitat and food for epiphytes and arthropods, flowers are an important source of nectar and pollen for honey bees	National emblem of Guatemala, Puerto Rico, and Equatorial Guinea; part of the coat of arms and flag of Equatorial Guinea; sacred symbol and important material (stuffing pillows and cushions) in Maya culture; importance in African folk medicine; fiber of global economic importance (used as an alternative to down as filling in mattresses, pillows, upholstery, zafus, stuffed toys and for insulation)	(www.monumentaltrees.com; Brokaw, 1987; Fridby, James, Olusegun, & Gabriel, 2011; Nicholas, 2011; Zidar & Elisens, 2009)
Patagonian cypress	<i>Fitzroya cupressoides</i>	Cupressaceae	Temperate forest	Wind	2.01	3,622	>100	150–200	unknown	Disturbance (fire, wind-fall) creating canopy gaps	Habitat and food for epiphytes (vascular plants and bryophytes) and arthropods	Declared as National Monument in Chile in 1976; threatened by overexploitation; protected in natural range	(Lara et al., 1999; Lara & Villalba, 1993)

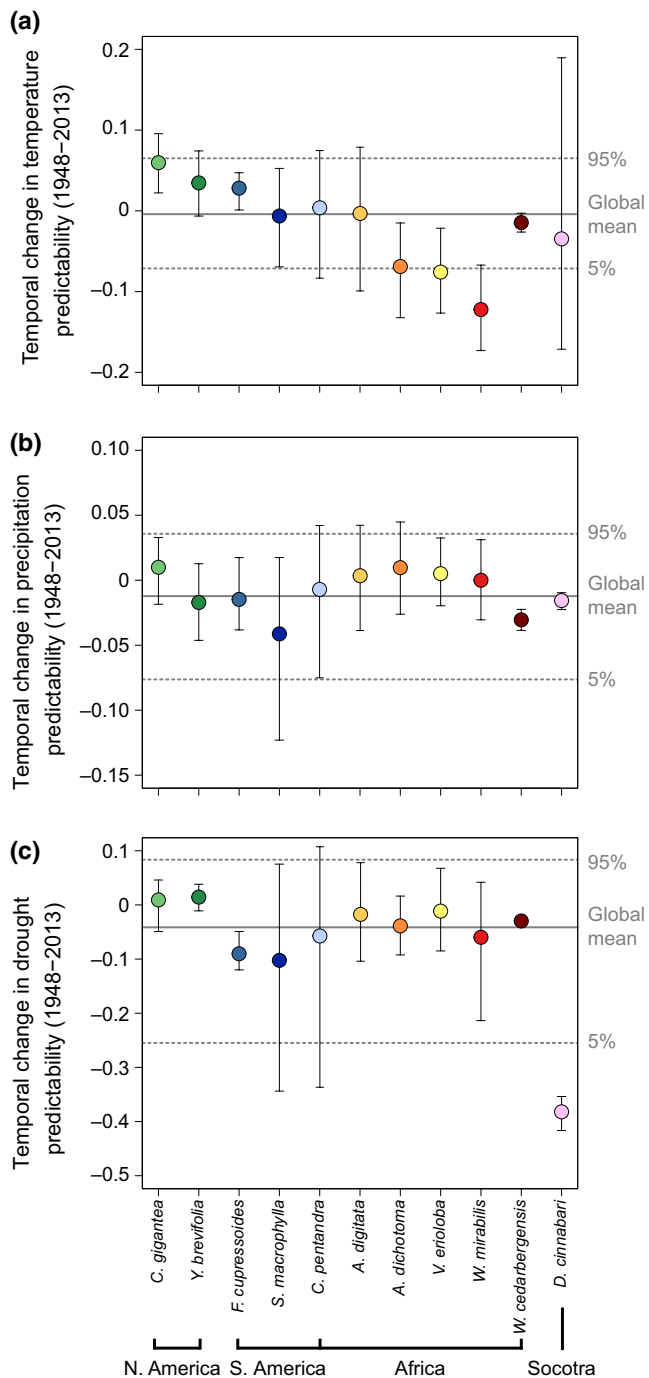


**FIGURE 2** Environmental and demographic features and processes of the syndrome of long-lived sporadic recruiters modulated by demographic storage components and competitive interactions with other, co-occurring species (not including the focal species). Pronounced demographic storage components (e.g., adult longevity) in combination with sporadic recruitment can cause strong disequilibrium conditions in demographic dynamics (i.e., extinction debts), affecting the long-term population viability of the focal species. These disequilibrium conditions have to be accounted in species and landscape management. Effects of the different factors on one another can be positive, negative or characterized by nonlinear effect-response relationships. Long-term population viability can be conserved/restored following a strategic, adaptive management scheme where management actions, monitoring objectives, public outreach, and objectives of mission-based research on the demographic features and processes characterizing long-lived sporadic recruiters are iteratively recalibrated (for details see Figure 4)

demographic feature is also reported to be relevant for species inhabiting environments that are not limited by water, such as tropical and temperate forests. In these regions adverse environmental conditions will be mainly biotically induced by competition with other species (e.g., competition for light) but environmental conditions can become sporadically favorable for recruitment when competition is removed (e.g., by disturbance-induced forest gaps increasing light availability for juvenile plants). In such cases disturbance pulses such as fire, windfall or flood events may create opportunities for recruitment in an otherwise highly competitive environment (Foster, Knight, & Franklin, 1998). The syndrome of long-lived sporadic recruiters can also apply to mast-fruiting, long-lived species like, for example, oaks (genus *Quercus*) across the Northern Hemisphere, or dipterocarps in Southeast Asia. Mast fruiting, defined as a synchronous and highly variable seed production among years within a population, is widespread in long-lived, perennial plants and is ultimately induced by a combination of sufficient resource availability sporadically co-occurring with a certain set of environmental cues (e.g., weather events, disturbance). The exact mechanisms driving mast-fruiting events are

still poorly understood (Pearse, Koenig, & Kelly, 2016). Mast fruiting events in long-lived tree species induced by climatically driven, abrupt changes in resource availability (e.g., drought, rain or fire events) have been reported by several authors (Ascoli et al., 2017, 2019; Piovesan & Adams, 2005). Generally, in all of the above-mentioned cases sporadic release from generally prevailing resource limitation induced by external stochastic climatic events or other sporadic disturbance pulses, and in some cases combined with internal, physiological drivers (for mast-fruiting) seem to induce sporadic recruitment by causing temporal variations in demographic rates (Figure 2).

We argue that demographic storage components of species, such as longevity and environmental resistance of adult (reproductive) plants to fluctuating (temporally unfavorable) environmental conditions, as well as seed and/or sapling bank longevity modulate the impact of sporadic recruitment on long-term population viability (Figure 2). These demographic storage components are the main features of the storage effect sensu Warner and Chesson (1985). The storage effect describes species that store their reproductive potential over multiples of their generation times when environmental



conditions impede successful recruitment but release this potential for recruitment when environmental conditions become sporadically favorable. This mechanism allows for species co-existence and long-term population viability, even in highly stochastic environments (Higgins, Pickett, & Bond, 2000). The higher longevity and environmental resistance of adults and the more pronounced seed or sapling bank longevity, the higher the chance to survive unfavorable conditions and reestablish, reproduce and initiate recruitment during favorable conditions. Consequently, occasional recruitment is still sufficient to maintain long-term population viability when species show strong demographic storage (Kaleme, 2003; Seymour, 2008; Wickens

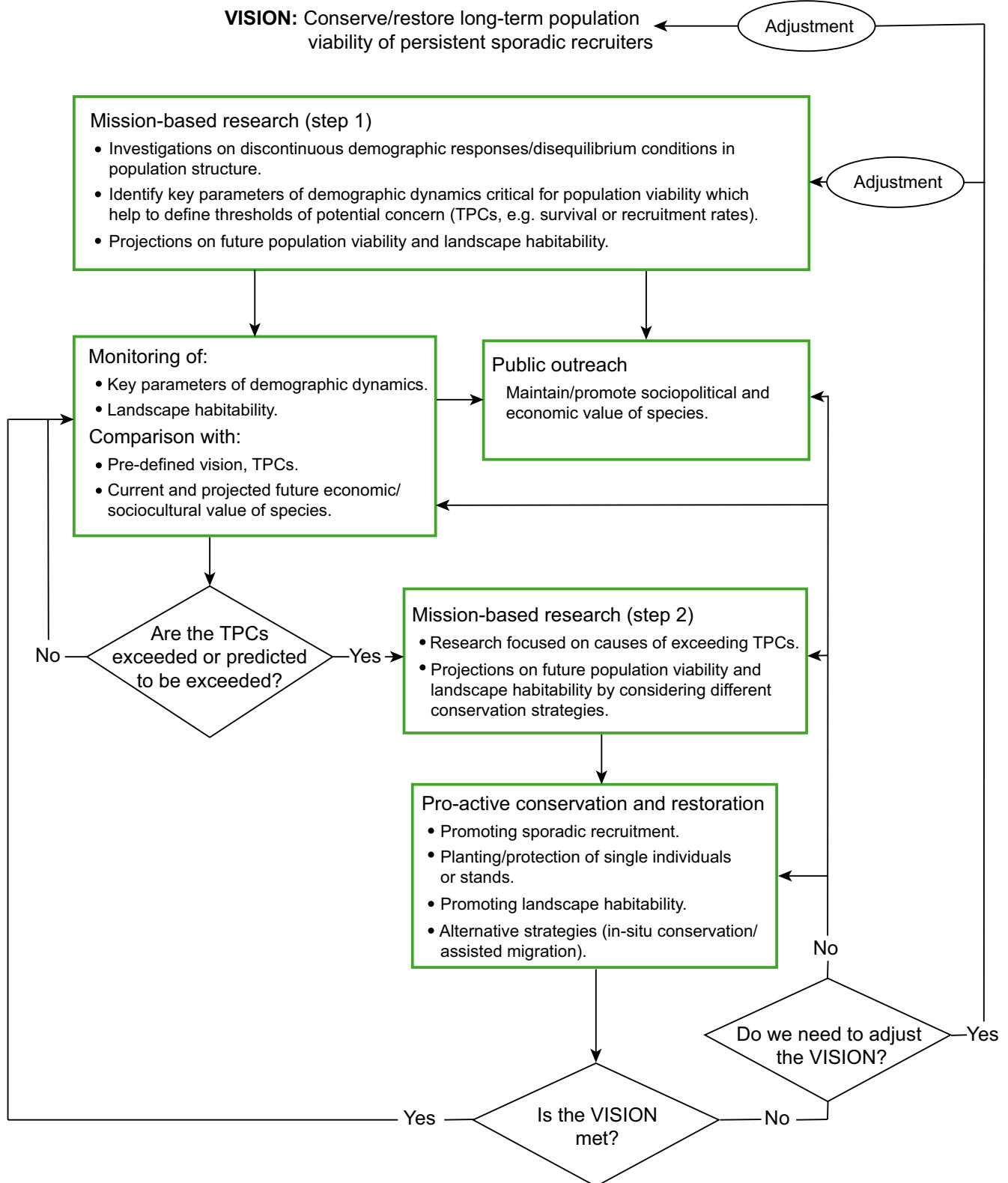
**FIGURE 3** Temporal changes in environmental predictability might have detrimental effects on the long-term population viability of long-lived sporadic recruiters by exceeding the species physiological limits or exhausting the storage effect. Depicted are temporal changes of the predictability of temperature (a), precipitation (b) and drought (potential evapotranspiration minus precipitation, c) as realized in the natural ranges of the set of iconic, long-lived sporadic recruiters summarized in Figure 1 and Table 1. Changes were quantified over a 65-year period (1948–2013). Species are grouped according to their continent of origin. Colored circles indicate mean value per species and whiskers of the 5% and 95% percentile based on the variation across the species natural ranges shown in Figure 1. The gray line illustrates the global mean of temporal change in climatic predictability with the dashed lines indicating the 5% and 95% percentiles. Climatic predictability as a combination of climatic constancy (variability) and periodicity was calculated according to (Jiang, Felzer, Nielsen, & Medlyn, 2017) by using the R package *hydrostats* (v.0.2.4; Bond, 2015) with climate data binned in  $n = 11$  classes for analyses (cf. Beissinger & Gibbs, 1993). As climate data we used long-term time series on mean monthly temperature and monthly total amount of precipitation and potential evapotranspiration with a spatial resolution of  $0.5^\circ$ – $0.5^\circ$  and a global extent (precipitation: Schneider et al., 2011; mean temperature: Fan & van den Dool, 2008, potential evapotranspiration: New, Hulme, & Jones, 1999). To assess temporal changes in temperature and precipitation predictability we estimated predictability for a 5-year window moved across the complete time series (1948–2013) in monthly steps. Temporal change was quantified as the slope of a simple linear regression model applied to the calculated predictability values

& Lowe, 2008). Such pronounced storage effects foster long-term population viability of sporadic recruiters in stochastic environments as exemplified by the set of long-lived, iconic plant species summarized in Table 1 (Gullison et al., 1996; Kaleme, 2003; Thomas, 1995; Wetschnig, 1997). Environmental stochasticity as the converse of environmental predictability is here defined as the amount of uncertainty and variability characterizing the temporal variation of a certain environmental signal (e.g., temperature or rainfall; Colwell, 1974).

Strong storage effects defining such species can lead to a decoupling of the environmental space currently occupied by the species and its regeneration niche (cf. Grubb, 1977). This might mean that the current species distribution reflects the spatial distribution of past recruitment events that occurred sporadically in space and time and, thus, might be in strong disequilibrium with current environmental conditions. These assumptions are analogous to the idea of remnant populations caused by trailing-edge disequilibrium (cf. Svenning & Sandel, 2013). In the following sections we discuss how ecological and demographic features characterizing long-lived sporadic recruiters can affect the species' sensitivity to anthropogenic global changes.

### 3 | ENVIRONMENTAL THREATS FOR SPORADIC RECRUITERS

Poor recruitment of a sporadic recruiter over a certain period of time is not necessarily a cause for concern. Variance in recruitment



**FIGURE 4** Strategic adaptive management scheme for the conservation/restoration of long-lived sporadic recruiters and their landscapes. The hierarchy of this scheme is structured in a general aim (ultimate goal) followed by more explicit objectives (green boxes) linked together in an adaptive management cycle of information, evaluation and adjustment. Thresholds of potential concern (TPCs) play a critical role in this adaptive cycle as they define limits of acceptable change of certain pre-defined indicators and, thus, articulate tangible (but adjustable) goals in the hierarchy. The structure of the scheme is based on (Rogers & Sherwill, 2008)



rates of competing species has been theoretically shown to favor species co-existence by precluding competitive exclusion (Warner & Chesson, 1985). This mechanism works as long as competing species can store reproductive potential over multiple generations and temporal variance of recruitment rates of the competing species are asynchronous. Plant species that can store reproductive potential over multiple generations can therefore profit from increasing variance (decreasing predictability) of environmental conditions (Higgins et al., 2000). Thus, sporadic recruiters—especially those with pronounced demographic storage—seem to tolerate or even depend on variable environments. This suggests that global environmental changes, such as increasing climatic variability might cause little harm on the population viability of these species. However, this might not be true under accelerating climate changes. The positive effect of environmental variability will reach a limit when environmental conditions exceed the physiological limits or exhausts the storage effect of a species, or when sporadically recruiting species become competitively too disadvantaged in comparison to other co-occurring species. Thus, both increasing as well as decreasing environmental variability and predictability can threaten the long-term population viability of species strongly relying on the storage effect. This is especially relevant as the changes in climatic (temperature, precipitation and drought) predictability observed during the last seven decades are not unidirectional, but show considerable spatial variation on a global scale and, thus, contrasting trends, i.e. increasing as well as decreasing climatic predictability (stochasticity) in the natural distribution areas of the discussed species (Figure 3).

Our analyses show that temporal changes in climatic predictability during the last seven decades were most pronounced for drought (potential evapotranspiration minus precipitation), followed by temperature and precipitation predictability. The observed bidirectional changes in environmental predictability are thereby likely to put the discussed species at both ends of the spectrum of favorable environmental conditions at risk. Additionally, only a subset of long-lived sporadic recruiters inhabit harsh environments and have a direct dependency on climatic variability and predictability, whereas others inhabit abiotically less stressful environments and depend on disturbance that is changing in the context of climatic and land-use changes (Goldewijk, 2001). Humans have altered disturbance regimes by, for example, fire suppression and flood regulation in large parts of the world. Such changes additionally threaten species reliant on a disturbance-induced release from generally prevailing resource limitation (MacDougall & Turkington, 2007). Consequently, global environmental changes are more likely to threaten than to favor sporadically recruiting species. Furthermore, many sporadically recruiting, long-lived species occur in extreme climates (e.g., dry climates), where further climate change might be particularly problematic (see below).

Pronounced, detrimental effects of global climatic changes on long-term population viability have been reported for several of the iconic examples listed in this paper. For the quiver tree (*Aloidendron dichotomum*), severe population collapses have been linked to climatic changes in recent decades (Foden et al., 2007). The effects

of climatic changes on long-term population viability are expected to be even more pronounced for the dragon's blood tree (*Dracaena cinnabari*) occurring on Socotra island with intensive disintegration of the remaining population anticipated within the next 30–77 years (Attorre et al., 2007). This is especially worrying as changes in the predictability of drought and temperature during the last decades are most pronounced in the natural range of *D. cinnabari* (Figure 3). For the Clanwilliam cedar (*Widdringtonia cedarbergensis*), a combination of historic exploitation, increasing temperature and aridity and increasing intensity and frequency of fires seems to have caused a persistent decrease in population viability, that is, a collapse of the storage effect (Farjon, February, Higgins, Fox, & Raimondo, 2013). Mortality rates of adult individuals of this species are assumed to be too high and recruitment rates too low to sustain long-term population viability under the current projections of future climatic changes (White et al., 2016). The same is assumed for the dragon's blood tree on Socotra where climatic changes in combination with strong herbivore pressure currently prevent natural recruitment (Attorre et al., 2007; Maděra et al., 2019). The threats can therefore be separated into two classes of effects: (a) environmental changes causing a reduction in the frequency of recruitment events; and (b) increased mortality of adults, saplings or seeds in the sapling and seed bank caused by an overshoot of the physiological limits or increased disturbance-induced mortality. All this can erode the storage effect. Changes in environmental variability and predictability causing changes in the temporal dynamics of resource availability (e.g., occurrence and intensity of rainfall events in arid environments, extent of intensive drought periods) thereby play a pivotal role. Importantly, even with a positive population growth rate, demographic and environmental stochasticity can still lead to local extinctions when the number of reproductive individuals in a population and, thus, reproductive output is too small to sustain long-term population viability (Hylander & Ehrlén, 2013).

Anthropogenic stressors such as over-harvesting for timber and non-timber products like fruits and seeds as well as land-use change and associated habitat loss have additional strong detrimental effects on the population viability of threatened plant species and, thus, also on long-lived sporadic recruiters. This has been shown to be the case for the big-leaf mahogany (Gullison et al., 1996), the Patagonian cypress (Lara, Fraver, Aravena, & Wolodarsky-Franke, 1999), the baobab (Dhillon & Gustad, 2004; Venter & Witkowski, 2010) and the camelthorn (Seymour, 2008). Thus, populations of long-lived sporadic recruiters might partly sustain viability with low, episodic recruitment under current environmental conditions, but ongoing climatic changes in combination with increasing land-use intensity and other anthropogenic stressors can reduce recruitment rates of these species below critical thresholds of population viability (e.g., Venter & Witkowski, 2013; Maděra et al., 2019). We expect these thresholds to strongly depend on species longevity and environmental resistance and therefore on the strength of demographic storage components. The more pronounced storage components are, due to, for example, high adult longevity and environmental resistance, the higher the likelihood of successful reproduction even for rare instances of favorable conditions

and, thus, the lower the probability of crossing a critical minimum of recruitment in the long run. However, if environmental resistance (or the ability to detect favorable environments) come at a significant resource cost, this cost may trade off with reproductive output, and successful reproduction may be increasingly limited.

Even when critical thresholds of population viability are exceeded, population breakdowns are likely delayed from decades to centuries for the discussed species due to the high longevity and low turnover rates (Kuussaari et al., 2009; Vellend et al., 2006). This can give rise to pronounced time lags, and thus, disequilibrium conditions in the demographic responses (Hylander & Ehrlén, 2013) or even pronounced extinction debts (Kuussaari et al., 2009) when environmental conditions favorable for recruitment become temporally too sparse. This may result in landscapes of the 'living dead' where plant individuals might be present but are already committed to extinction due to failing recruitment (Janzen, 1988; Manning, Fischer, & Lindenmayer, 2006). This seems to be the case for the Clanwilliam cedar in South Africa and the dragon's blood tree on Socotra island. Recent anthropogenic habitat transformation on oceanic islands has caused sharp declines in recruitment of long-living species (whether or not these are sporadic recruiters). Yet these changes will only propagate into visible effects in the population structure and the abundance of adult individuals in multiple decades, or even hundreds of years, because of the species' pronounced longevity (Kueffer & Kaiser-Bunbury, 2014). A prominent oceanic island example is the coco de mer palm, *Lodoicea maldivica*, which is endemic to the Seychelles (Rist et al., 2010). Thus, special emphasis should be put on recently modified habitats that are inhabited by plant species with pronounced longevity.

Humans can nevertheless play a pivotal role in maintaining or facilitating viable populations of sporadically recruiting, long-lived species. Tree density and recruitment of baobabs are, for example, reported to be favored around human settlements by active (e.g., planting in orchards) and passive distribution (e.g., seeds as remains of edible fruits are unintentionally dispersed with garbage) as well as by active protection of juvenile plants (e.g., from damage by livestock). This is done to maintain sources of economically relevant products like food (fruits, leaves), other non-timber products (cosmetics, lifestyle products) or bark and wood for construction etc. (Dhillon & Gustad, 2004; Duvall, 2007). In general, the commercial and cultural values associated with a particular species seems to be a key factor in determining whether net human impact on population viability is positive or negative.

#### 4 | OBJECTIVES FOR CONSERVATION AND RESTORATION

Since sporadic recruitment heavily relies on episodic release from otherwise prevailing resource limitation, such species follow a risky strategy when considering the accelerating environmental changes projected for the coming decades to centuries. Traditional conservation schemes usually focus on static environments and assume equilibrium conditions to prevail in ecosystems (Kuussaari et al., 2009; Ladle & Gillson, 2009; Simberloff,

2014). Thus, pronounced temporal variability in the demographic responses to environmental changes as well as a sensitive dependence on stochastic environments is insufficiently covered by these traditional schemes. This puts the long-term population viability of sporadically recruiting, long-lived species at risk. We therefore argue that alternative, more dynamic approaches of species and landscape management are needed when such species become threatened. The importance of dynamic, adaptive conservation schemes increases with the strength of demographic storage components characterizing the species demographic responses, this is especially relevant for the set of long-lived, iconic plant species summarized in this study.

In the following sections we outline an integrative, adaptive conservation framework to account for the temporally lagged, demographic responses of sporadically, long-lived species to environmental changes and provide advice for the practical implementation of effective species and landscape management. We achieve this by applying the idea of a strategic adaptive management (SAM, Biggs & Rogers, 2003). These dynamic management approaches were developed for the management of whole ecosystems (e.g., South African savannas), but can be similarly applied to long-lived sporadic recruiters.

Strategic adaptive management schemes are structured around a hierarchy of objectives. At the top level a general set of normative goals serve as the ultimate aims of a specific conservation or restoration project, followed by lower-level objectives which increase in explicitness (Figure 4). Thresholds of potential concern (TPCs; sensu Biggs & Rogers, 2003) define limits of acceptable change of certain pre-defined indicators (e.g., recruitment or survivorship rates in a certain region for a defined period of time), representing the lower level objectives in the objectives hierarchy. When a TPC is reached or predicted by modelling to be reached in the near future, detailed assessment of the current ecological state is triggered and management actions are induced (if necessary) in accordance with the pre-defined objectives. Although pre-defined, TPCs will be recalibrated based on new assessments of the causes of reaching a certain TPC as part of the adaptive management cycle. Similarly, management decisions and actions should be permanently compared with the set goals and (if necessary) recalibrated. This should happen by using an iterative evaluation of the current and projected future population structure and landscape suitability (see Figure 4).

Relevant TPCs strongly depend on species-specific demographic characteristics and therefore have to be defined case-by-case. Furthermore, effective TPCs have to account for the socio-cultural and economic background and the landscape settings of the region of interest and, thus, cannot simply be generalized. Detailed understanding about the key physiological and demographic processes linked to the emergence of the syndrome of long-lived sporadic recruiters are a prerequisite to set up sensible TPCs. However, critical knowledge will often be missing. The first step for effective management is to close critical knowledge gaps regarding the key demographic characteristics of the focal

species. These knowledge gaps can be filled by careful field studies as part of mission-based research programs that run in parallel to the other components of the strategic, adaptive management program (Figure 4). A second step would be to screen the socio-cultural, economic, and landscape backgrounds for the specific project. Such screening would yield information on the socio-cultural and economic importance of the target species in the region of interest and beyond, and can be obtained by exploring the traditional ecological knowledge (Gadgil, Berkes, & Folke, 1993) of local communities by conducting surveys among local people (Barnhardt & Kawagley, 2005; Huntington, 2000), for example. Efficient public outreach, and long-term programs monitoring the demographic dynamics and the economic and cultural importance of the target species are necessary to meet the pre-defined goals (cf. Pierson & Turner, 1998). This is especially important for iconic species with pronounced storage effects. Another important task would be to quantify how changing environmental predictability as a key driver of sporadic recruitment will affect long-term population viability of the focal species. Space-for-time investigations of species physiological and demographic characteristics in differently stochastic and variable environments could, for example, be used to infer recruitment dynamics and other important information on species reactions when recruitment events happen too rarely to allow efficient temporal monitoring. This might be often the case especially for long-lived sporadic recruiters characterized by strong demographic storage. Such space-for-time investigations would for example study species physiology, demographic structure and recruitment of populations growing under different environmental conditions represented in the current distribution range of the target species and which reflect future conditions projected for the target region. However, using information from space-for-time investigations to replace temporal monitoring has to be done carefully. For example, inference might be more reliable if the differences found between populations exposed to different levels of stochasticity and variability are plastic than if they are genetic. This is usually investigated with common garden experiments for herbaceous species but might be challenging for long-lived plant species.

One of the most important challenges of managing sporadically recruiting, long-lived species (as well as other long-lived species) is that adult population densities do not necessarily reflect long-term viability of the species—especially in times of strong environmental changes. Pronounced temporal lags in the demographic responses of long-lived sporadic recruiters caused by strong demographic storage pave the way for pronounced extinction debts. Challenges for species conservation caused by extinction debts (i.e., not recognizing it in management schemes) might then be particularly relevant. In such cases, red list assessments that mainly build on the distribution data of adult individuals without considering recruitment might become particularly problematic. However, temporal discontinuities in population structure can provide an opportunity to restore population viability even when populations might have passed critical thresholds of population

viability towards quasi-extinction because of adult, reproductive individuals still being present (Hylander & Ehrlén, 2013; Kuussaari et al., 2009). Such extreme storage gives the conservation manager more time to develop and implement plans, but this also requires stronger institutional memory to ensure that projects do not fail when a project leader moves jobs. Pro-active restoration or conservation practices like the planting or protection of single individuals or stands might be a necessary complementary management strategy to overcome temporal discontinuities and bottlenecks in recruitment (Adolt et al., 2013; Sanchez, Osborne, & Haq, 2011; Venter & Witkowski, 2013). This is done for the critically endangered Clanwilliam cedar and the dragon's blood tree, which are both subject to extensive ex situ conservation (cultivation in local nurseries and botanical gardens; Adolt et al., 2013; Farjon et al., 2013). Nevertheless, attempts to strengthen local populations of the Clanwilliam cedar by replanting from ex situ conservation show low rates of success up to now (Mustart, 2008). This is most likely due to the inability to push population viability back beyond critical thresholds, which is necessary for sustainable, successful recruitment of the species. Adaptive management schemes will fail in sustaining long-term population viability of such species when demographic storage components are not sufficiently accounted for, as might be the case for the Clanwilliam cedar. Thus, understanding and restoring the key mechanisms that ensure species long-term population viability on evolutionary time scales is a prerequisite for successful restoration with the general aim to achieve self-sustaining populations of the focal species.

Accelerating climatic changes represent a major challenge for the conservation/restoration of long-lived, sporadically recruiting species. Less conventional conservation practices like assisted migration into new landscapes with more suitable landscape features and future climates need to be considered when long-term population viability cannot be ensured by in situ management in the original landscape (see White et al., 2016 for the Clanwilliam cedar). Assisted migration might become especially relevant in the face of anthropogenic climate change with unprecedented changes of climatic conditions into climatic conditions unseen for millions of years (Burke et al., 2018). However, sporadically recruiting species anthropogenically moved beyond their current range into new biogeographic realms can also cause serious ecological problems in the recipient regions as exemplified by the camelthorn acacia (*Vachellia erioloba*). This species is declared as invasive after it was introduced as an ornamental plant to Australia (Victoria State Government, 2018). However, risks related to assisted migration are assumed to be less relevant when translocation activities do not cross biogeographical boundaries (Hoegh-Guldberg et al., 2008). Nevertheless, the potential ecological and socio-economic risks of assisted migration must be carefully evaluated before such alternative conservation action is undertaken.

Species adapt over evolutionary time scales to the environments they inhabit. Temporal and spatial variability of environmental conditions shape species physiology, ecology, and evolution (Janzen, 1967; Quintero & Jetz, 2018; Sheldon, Huey, Kaspari, &

Sanders, 2018). Species experiencing high environmental variability (e.g., variability in water availability) are forced to adapt, for example, their physiology, demography or life history to maintain fitness and, thus survival in variable environments (Janzen, 1967). The set of species discussed in this work show a set of rather exceptional, demographic characteristics. For these species we highlight the importance of alternative, more dynamic approaches in species and landscape management to account for disequilibrium dynamics in species demography. This might lead to the (unwarranted) conclusion that those species are ecological peculiarities and, thus, the conservation framework presented here might be of limited use. However, similar mechanisms important for the long-lived sporadic recruiters discussed are also reported to be important in less extreme forms of sporadic recruitment for other plant species like various acacias in South Africa (*Vachellia karroo*, *V. nigrescens* and *V. nilotica*) or *Callitris glaucophylla* in Australia, as well as for various desert plant species in North America (Austin & Williams, 1988; Bowers et al., 2009; Staver, Bond, & February, 2011). Populations of these species are also dominated by even-aged individuals as an outcome of generally limited but sporadically successful recruitment. However, demographic storage components such as adult longevity are less pronounced for these species resulting in a lower probability of disequilibrium conditions (e.g., extinction debts) characterizing species demographic dynamics. Thus, infrequent recruitment and especially its interplay with demographic storage components can play out on various time scales and, thus, might be of different importance in species and landscape conservation and restoration. The framework developed here to describe the apparently demographic peculiarity of a set of iconic species may therefore be of widespread relevance for raising awareness of lagged demographic responses and for adapting existing or developing new, effective management practices to account for disequilibrium responses such as extinction debts under ongoing global changes. Accounting for disequilibrium responses which occur in nature in different intensities is most certainly a key challenge for nature conservation and resource management in the Anthropocene (Sprugel, 1991). Conserving or restoring natural disturbance regimes (Perino et al., 2019) will be one important component to master this challenge.

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#### AUTHOR CONTRIBUTION

A.H.S. and S.I.H conceived the idea for the manuscript. A.H.S. and S.D.H.I created the figures. A.H.S. analyzed the data and wrote the manuscript with substantial contributions by all co-authors.

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