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The edaphic control of plant diversity

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Abstract

Background: The central thesis of plant ecology is that climate determines the global distribution of vegetation. Within a vegetation type, however, finer-scale environmental features, such as the physical and chemical properties of soil (edaphic variation), control patterns of plant diversity and distributions.

Aims: Here, we review the literature to provide a mechanistic framework for the edaphic control of plant diversity. First, we review three examples where soils have known, prevalent effects on plant diversity: during soil formation, on unusual soils and in regions with high edaphic heterogeneity. Second, we synthesize how edaphic factors mediate the relative importance of the four key processes of community assembly (speciation, ecological drift, dispersal and niche selection). Third, we review the potential effects of climate change in edaphically heterogeneous regions. Finally, we outline key knowledge gaps for understanding the edaphic control of plant diversity. In our review, we emphasize floras of unusual edaphic areas (i.e., serpentine, limestone, granite), because these areas contribute disproportionately to the biodiversity hotspots of the world.

Taxa: Terrestrial plants.

Location: Global.

Conclusion: Edaphic variation is a key driver of biodiversity patterns and influences the relative importance of speciation, dispersal, ecological drift, niche selection and interactions among these processes. Research is still needed to gain a better understanding of the underlying mechanisms by which edaphic variation influences these community assembly processes, and unusual soils provide excellent natural systems for such tests. Furthermore, the incorporation of edaphic variation into climate change research will help to increase the predictive power of species distribution models, identify potential climate refugia and identify species with adaptations that buffer them from climate change.

KEYWORDS

community assembly, edaphic, geodiversity, geology, gradient, heterogeneity, macroecology, soil

1 | THE EDAPHIC FACTOR

Geology shapes plant diversity via its influence on the chemical and physical properties of soils (Kruckeberg, 2004). The weathering of parent material determines soil properties including texture, clay

content, water-holding capacity, exchange capacity and the quality of the mineral ions themselves (Jenny, 1941; Troeh & Thompson, 2005). Soil parent material is thus a major driver of plant nutrient availability (Augusto, Achat, Jonard, Vidal, & Ringeval, 2017; Ferwerda et al., 2006; Vestin, Nambu, van Hees, Bylund, & Lundström, 2006),

and soil is the medium in which most terrestrial plants evolve, grow and derive their nutrients and water supply. As a result, edaphic variation is second only to climate as a major determinant of plant distributions (Kruckeberg, 1986; Rajakaruna, 2004). For example, regions of complex geologies give rise to more than half of the biodiversity hotspots of the world and contribute disproportionately to global diversity (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). The limestone grasslands of Europe, the karstic *mogotes* of the Caribbean, the Appalachian shale barrens, the gypsum outcrops across Spain, Mexico and the south-western USA, and the serpentine floras of the Mediterranean, Cuba, New Caledonia and California (Damschen, Harrison, Ackerly, Fernandez-Going, & Anacker, 2012) exemplify the edaphic control of plant diversity.

Although the idea that edaphic factors control plant distributions is not new (see Grubb, 1989; Richter & Babbar, 1991), a growing body of research over the last two decades suggests that edaphic factors play a larger role in plant community assembly and plant diversity gradients than previously considered and warrant deeper consideration. For example, microbial biogeography is controlled primarily by edaphic variables (Fierer & Jackson, 2006) which, in turn, have cascading effects on plant diversity and productivity (Bever et al., 2010; Van Der Heijden, Bardgett, & Van Straalen, 2008). Furthermore, soil infertility alters ecosystem responses to climatic variation, resulting in long-term resistance to climate change (Grime et al., 2008). Edaphic heterogeneity can also control ecological divergence and species diversification (Fine, Daly, & Cameron, 2005; Rajakaruna, 2018), resulting in variation in species composition and habitat specialization across broad spatio-temporal scales.

Importantly, edaphic properties are one component of geodiversity, which is defined as “the natural range of geological (rocks, minerals, fossils), geomorphological (landforms, topography, physical processes), soil and hydrological features”, including “their assemblages, structures, systems and contributions to landscapes” (Gray, Gordon, & Brown, 2013). The concept of geodiversity is central to biodiversity conservation and climate adaptation strategies (known as “Conserving Nature’s Stage”; Beier, Hunter, & Anderson, 2015; Hjort, Gordon, Gray, & Hunter, 2015; Lawler et al., 2015) and is increasingly recognized as an important factor for explaining biodiversity gradients (Antonelli et al., 2018; Bailey, Boyd, & Field, 2018; Hjort, Heikkinen, & Luoto, 2012; Parks & Mulligan, 2010). Although geodiversity has many components, in this review we emphasize a single facet of geodiversity: edaphic variation. Our emphasis on edaphic variation thus bridges two bodies of literature: plant community assembly and geodiversity. Plant community assembly theory rarely considers geodiversity explicitly (but see Harrison, 2011), whereas the geodiversity–biodiversity literature rarely considers the underlying assembly mechanisms that drive biodiversity patterns (but see Bailey, Boyd, Hjort, Lavers, & Field, 2017; Hjort et al., 2012; Lawler et al., 2015; Parks & Mulligan, 2010). In this review, our primary aim is to help unify these fields by expanding on a shared commonality, soils.

Research emphasizing the edaphic control of plant diversity has primarily focused on three distinct areas of study: soil

chronosequences (pedogenesis), unusual soils and regions of high edaphic heterogeneity. The edaphic control of plant diversity across spatio-temporal scales is most apparent during pedogenesis (the process of soil formation; Jenny, 1941). The latitudinal diversity gradient, for example, coincides with a global gradient in soil development (Huston, 2012; Sanchez, 1977). Tropical soils are among the most ancient and weathered soils in the world yet support most of the world biodiversity. In contrast, younger soils of high-latitude regions support lower total species richness after recent deglaciation. Other soil chronosequences around the world reveal a trend of increasing plant species richness with increasing soil age (e.g., Crews et al., 1995; Laliberté et al., 2013; Wardle, Bardgett, Walker, Peltzer, & Lagerström, 2008). This may be attributable largely to predictable changes in nutrient availability during pedogenesis, which are consistent across ecosystems, climates and parent material (Peltzer et al., 2010).

Unusual soils provide a special case where soil properties (and parent material) differ dramatically from nearby, often adjacent, soils. These soils tend to be unusually harsh (low in nutrient and water availability) and are often referred to as “azonal”, in contrasted to “zonal”, more fertile soils in the same region (Damschen, Harrison, Going, & Anacker, 2011). Unusual soils are distributed globally (see Figure 1), tend to occur in relatively small, spatially isolated outcrops and support distinct plant communities with unusually high rates of endemism, as is found on serpentine soils of Cuba (Brooks, 1987), granite inselbergs of South America (Porembski, Seine, & Barthlott, 1997) and limestone outcrops of Southeast Asia (Clements, Sodhi, Schilthuizen, & Ng, 2006), to name a few. In California, serpentine endemics comprise > 10% of plant species richness, even though serpentine is < 2% of its surface area (Safford, Viers, & Harrison, 2005). Globally, 68% of biodiversity hotspots identified by Myers et al. (2000) and Mittermeier et al. (2004) occur on unusual soils (Damschen et al., 2011), suggesting a key role for unusual soils in biodiversity conservation. The high rates of endemism, which are characteristic of unusual soils, suggest that adaptation to unique edaphic properties is an important stimulus for speciation. Indeed, case studies of endemism on unusual soils (e.g., Antonovics & Bradshaw, 1970) are classic examples of natural selection driven by edaphic properties. Specifically, there is strong evidence for a direct relationship between adaptation to a particular substrate and reproductive isolation even without strong barriers to gene flow (Rajakaruna, 2004), supporting the idea that unusual soils play a direct role in evolutionary diversification (Kruckeberg, 1986).

Although unusual soils provide an extreme case of adaptation and speciation in response to edaphic properties, edaphic heterogeneity (i.e., pedodiversity; Ibáñez & Bockheim, 2013) also contributes to patterns of plant diversity. The spatial environmental heterogeneity hypothesis assumes an inverse relationship between latitude and environmental complexity (Pianka, 1966). In fact, variation in soil properties was a major component of original formulation by Ricklefs (1977) of the spatial heterogeneity hypothesis. Spatial heterogeneity can contribute to speciation by fragmenting populations and restricting gene flow, allowing populations to follow independent

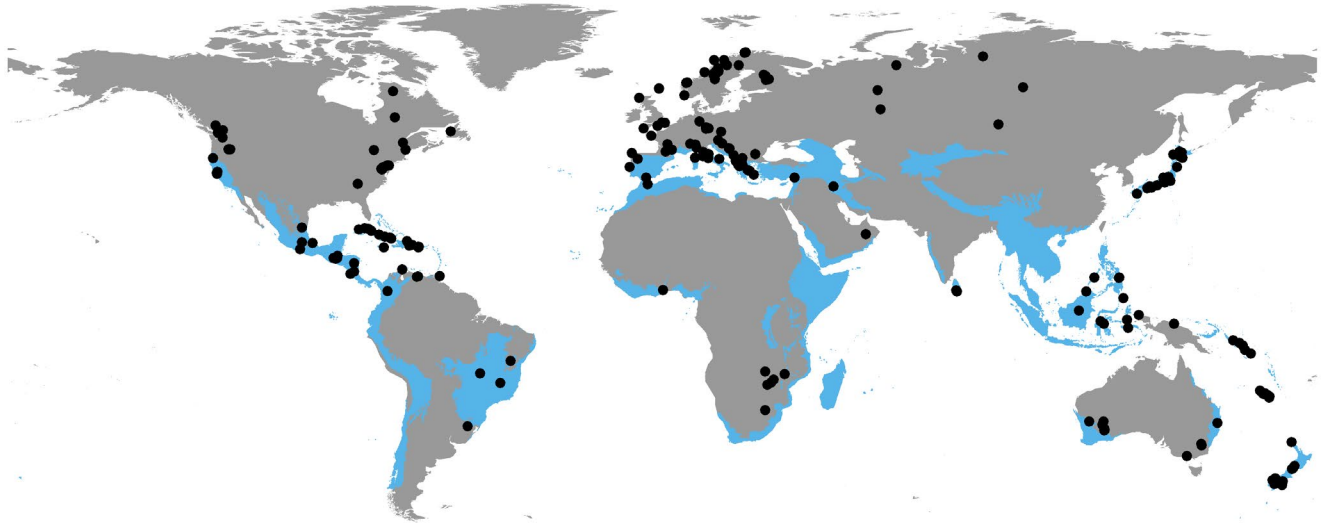


FIGURE 1 More than half of the world's biodiversity hotspots (shaded in blue; Mittermeier et al., 2004; Myers et al., 2000) are associated with unusual soils, pointing to the edaphic control of global biodiversity patterns and the importance of conserving unusual soils to protect biodiversity. Biodiversity hotspots are locations where "exceptional concentrations of endemic species are undergoing exceptional loss of habitat" (Myers et al., 2000), underscoring the fact that although unusual soil formations harbour rare and unique biota, they are also highly threatened. Major serpentine outcrops (shown here as points) are found on every continent (except Antarctica, not shown), many of which are located within biodiversity hotspots. Serpentine locations are compiled from Brooks (1987) and Roberts and Proctor (1992); hotspot data are from Conservation Synthesis, Center for Applied Biodiversity Science at Conservation International (2011)

evolutionary trajectories (Gill et al., 2015). Spatial heterogeneity in edaphic aridity, for example, was proposed as a primary factor in angiosperm evolution (Axelrod, 1972), and early studies provided evidence for the sorting of plants into floristically distinct, edaphically determined communities in species diverse places, such as the Amazon (e.g., Gentry, 1981).

Moreover, studies accounting for issues of scale and sparse sampling are accumulating widespread evidence for the role of edaphic variation on continental-wide patterns of plant diversity, distribution and speciation in some of the most diverse forests in the world (e.g., Fine et al., 2005; Fine & Kembel, 2011; Phillips et al., 2003; ter Steege et al., 2006; Tuomisto et al., 1995). Equatorial regions are known for exceptional variation in soil biogeochemistry at local and regional scales because of differences in soil age, soil chemistry and the rates of erosion and tectonic uplift (Townsend, Asner, & Cleveland, 2008). Outside of the tropics, edaphic heterogeneity accounted for most of the variation in plant species richness of U.S. eastern deciduous forests (Burnett, August, Brown, & Killingbeck, 1998; Nichols, Killingbeck, & August, 1998) and much of the variation in species distributions across mixed evergreen forests of the Pacific Northwest (Whittaker, 1960). In other temperate regions, the diversity of landforms and hydrological features (which impact soil type and soil nutrient availability) significantly improved plant species distribution models (Bailey et al., 2018; Hjort et al., 2012) and explained patterns of plant diversity (Tukiainen, Bailey, Field, Kangas, & Hjort, 2017).

These studies and others note the importance of environmental heterogeneity, but generalizable mechanisms are not yet well understood. Whittaker (1960) noted the tendency for plant species to shift in distribution depending on soil type, citing the law of geoeological

distribution (Boyko, 1947) and the law of relative site constancy (Walter & Walter, 1953). Whittaker's (1960) mountain gradient analyses arguably foreshadowed the quantitative study of the edaphic control of plant diversity (e.g., Grace, Harrison, & Damschen, 2011). Of course, von Humboldt's (von Humboldt & Bonpland, 1807) vivid descriptions of plant biogeography across mountains created an enduring platform for understanding interactions between edaphic variation and plant diversity and, more broadly, geodiversity and biodiversity (Schrodt, Santos, Bailey, & Field, 2019). Mountains are a special case where topographical, hydrological, edaphic, climatic and other processes differ dramatically across short distances, contributing to both high local and regional diversity (Rahbek, Borregaard, Antonelli, et al., 2019; Rahbek, Borregaard, Colwell, et al., 2019). Mountain biodiversity is tightly linked to bedrock geology. Interestingly, all hyperdiverse mountain regions are rich in mafic and ultramafic rocks (Rahbek, Borregaard, Antonelli, et al., 2019), the parent material for unusual soils.

Despite the large body of research (above) highlighting the prominent role of soils in controlling plant diversity, we lack a clear framework for understanding the mechanisms by which this occurs and how these processes mediate plant community responses to environmental change. Often, edaphic heterogeneity and, more broadly, geodiversity are excluded from macroecological and distributional studies, which tend to focus primarily on temperature and precipitation gradients (e.g., Gaston, 2000; Pianka, 1966). Renewed interest in geodiversity, both in conservation research and as a predictor of biodiversity patterns, can be seen in the increasing number of studies demonstrating the contribution of geodiversity to patterns of plant diversity and turnover at varying spatial scales

(e.g., Bailey et al., 2017; Tukiainen, Kiuttu, Kalliola, Alahuhta, & Hjort, 2019; Zarnetske et al., 2019). Although these studies are important in establishing tighter linkages between geodiversity and macroecology, a looming challenge will be to disentangle the mechanisms that underlie the relationship between geodiversity and biodiversity. In the following sections, we discuss how edaphic factors influence plant diversity patterns by mediating the relative importance of the four community assembly processes (Box 1; after Vellend, 2016) and outline the importance of edaphic controls for understanding how plant communities might respond to climate change. We limit this review to terrestrial plants owing to (a) their strong and universal interactions with edaphic properties, (b) the depth of research on plant community assembly and responses to climate change, and (c) the fact that plants are the base of all terrestrial ecological systems. Importantly, as the rate of climate change and land degradation increases, predicting the response of plant communities in edaphically diverse regions is a crucial next step for preserving and restoring ecosystem services.

2 | KEY PROCESSES BY WHICH EDAPHIC VARIATION DRIVES PLANT DIVERSITY

The processes that determine plant distributions and diversity patterns operate over a range of spatial and temporal scales (Crawley & Harral, 2001; Levin, 1992), which has caused considerable debate about the predictability of diversity gradients (Lawton, 1999; Ricklefs, 2008). Vellend (2016) challenged these criticisms and proposed that patterns of diversity could be explained by understanding four higher-order processes of community assembly: speciation (the formation of new species); dispersal (the movement of individuals through space); ecological drift (changes in species relative abundances that are random with respect to species identities); and niche selection (changes in species relative abundances owing to abiotic and biotic conditions that give rise to deterministic fitness differences between species) (Vellend, 2016). Here, we outline how edaphic variation influences each of these four processes to give rise to observed patterns of plant diversity (Box 1).

2.1 | Speciation

In response to the historical emphasis on local-scale processes in driving patterns of biodiversity, Ricklefs (1987) and others (i.e., Belmaker & Jetz, 2012; Harrison & Cornell, 2008; Mittelbach & Schemske, 2015) highlighted the importance of processes occurring at broader spatial and temporal scales. A key component of these advances is that the size and composition of the regional pool from which communities assemble are key drivers of biodiversity patterns (Eriksson, 1993; Patrick & Brown, 2018; Spasojevic, Catano, LaManna, & Myers, 2018; Zobel, 1997) and that the size and composition of the regional pool are influenced by speciation (in addition to immigration and ecological drift; Zobel, 2016).

Importantly, edaphic heterogeneity (or pedodiversity *sensu* Ibáñez, De-Albs, Bermúdez, & García-Álvarez, 1995) and the presence of unusual soils will create novel opportunities for speciation. For this reason, unusual soils have been proposed as a model system for the study of speciation (Rajakaruna, 2018). When the edaphic properties of a substrate are spatially heterogeneous, opportunities for colonization by different species and the events leading to speciation can occur (Kruckeberg, 1986). In the case of unusual soils, colonization can occur via local adaptation (ecotypes) or by phenotypic plasticity (Hereford, 2009; Palacio-López, Beckage, Scheiner, & Molofsky, 2015). Ecotypes are a crucial stage in the speciation process (Via, 2009), and ecotypic differentiation along sharp edaphic gradients provides some of the best evidence for natural selection (Rajakaruna & Whitton, 2004). Speciation from ecotypic differentiation is a multi-step process that begins with (a) the acquisition of edaphic tolerances (ecotypes), followed by (b) either gradual divergence of populations or disruptive selection, which results in (c) self-perpetuating populations with reduced gene flow owing to intrinsic (genetic) or extrinsic (edaphic) factors, resulting in (d) incipient reproductive isolation, and finally, if further isolations occur, (e) speciation (Kruckeberg, 1986). Although substantial support exists for ecotypic differentiation and species-level endemism among flowering plants on unusual soils (O'Dell & Rajakaruna, 2011), such patterns are much less documented for ferns, gymnosperms, mycorrhizal fungi, lichens or bryophytes (Rajakaruna, Boyd, & Harris, 2014). It is important to note that the role of phenotypic plasticity in the evolution of new species is still debated (Fazlioglu, Wan, & Bonser, 2017; Ghalambor, McKay, Carroll, & Reznick, 2007), and it is unclear how phenotypic plasticity on unusual soils or in edaphically diverse areas might contribute to speciation (De Jong, 2005).

Via its effects on speciation, edaphic variation can influence both regional and local diversity patterns. By creating opportunities for speciation (outlined above), areas that are more edaphically diverse are likely to have greater regional richness, and this regional pool of species will also be likely to be more functionally diverse (Harrison, Safford, Grace, Viers, & Davies, 2006). Although increasing the size of regional pools will increase regional diversity, the functional diversity of regional species pools can have cascading impacts on local patterns of diversity. Specifically, species pool functional diversity can influence the relative importance of local assembly processes, whereby more functionally diverse pools increase opportunities for species to sort across edaphic gradients (Patrick & Brown, 2018; Spasojevic et al., 2018).

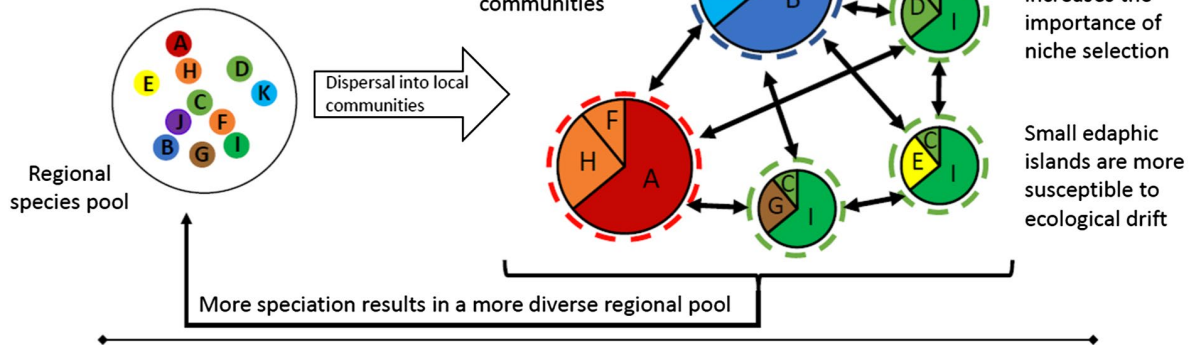
2.2 | Dispersal

Dispersal plays a key role in both regional (i.e., immigration) and landscape patterns (i.e., source-sink dynamics) of diversity (Leibold et al., 2004; MacArthur & Wilson, 1967; Vannette & Fukami, 2017). The influence of edaphic variation on dispersal depends on both the spatial distribution of soils across the landscape (Holyoak, Leibold, Mouquet, Holt, & Hoopes, 2005; Leibold et al., 2004; MacArthur &

Box 1 Conceptual framework for how edaphic variation influences the relative importance of speciation, dispersal, ecological drift and niche selection

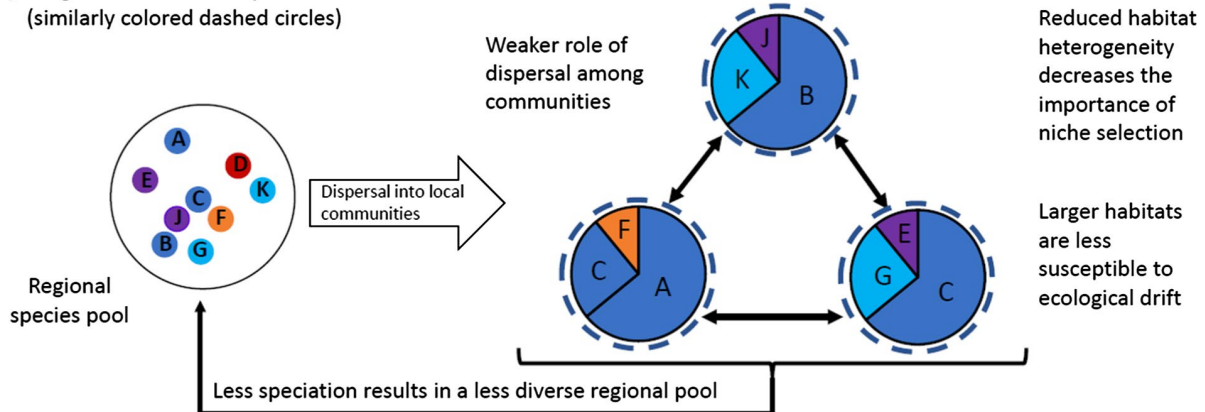
(a) Region of high edaphic variation

(differently colored dashed circles)



(b) Region of low edaphic variation

(similarly colored dashed circles)



A conceptual framework is presented that links edaphic variation, drivers of community assembly and patterns of diversity at regional (white circles with small coloured circles) and local (coloured pie charts) scales. Letters represent different species in each region, and colours represent functional traits. In this example, two regions (A and B) differ in edaphic variation, resulting in differences in environmental conditions among local communities (dashed coloured rings around circles). This difference in edaphic variation has cascading influences on the dominant assembly processes. Edaphic variation and the presence of unusual soils will create new opportunities for speciation, influencing both regional and local diversity patterns. By creating opportunities for speciation, areas that are more edaphically diverse (A) will have greater regional richness and regional functional diversity than areas with low edaphic variation (B). By creating spatial variation in the environment, edaphic variation will strongly influence dispersal (arrows between pie charts) and the resulting patterns of diversity. If patches are close enough in space to allow dispersal, such heterogeneity might increase diversity through spatial storage effects. In other cases, patches might be far enough apart to reduce connectivity among patches, which might contribute to speciation or increase the probability of demographic stochasticity, potentially resulting in extinctions and a reduction in diversity. Small edaphic islands (green circles in A) might support smaller population sizes, increasing the probability of demographic stochasticity and increasing the importance of ecological drift. Finally, edaphic variation has strong and varied effects on niche selection. Within a trophic level, niche selection will result in species sorting across habitats (colours of pie slices match coloured rings) and alter the relative importance of biotic interactions. Across trophic levels, both antagonistic and mutualistic interactions influence biodiversity patterns where herbivore pressure might be greater on unusual soils, but the reduced pathogen load and increased prevalence of symbioses might benefit many species.

Wilson, 1967) and the environmental conditions of a given location (Ozinga, Bekker, Schaminee, & Van Groenendael, 2004). The impact of edaphic variation on dispersal is likely to be more pronounced on unusual soil types restricted to island-like habitats (Harrison & Rajakaruna, 2011; Spasojevic, Damschen, & Harrison, 2014). Dispersal can connect similar communities on spatially discontinuous edaphic islands, which can rescue populations from local extinction owing to localized abiotic factors or biotic interactions (source-sink dynamics; Amarasekare, Hoopes, Mouquet, & Holyoak, 2004; Anderson & Geber, 2010; Mouquet & Loreau, 2003). Moreover, the isolated nature of edaphic islands can create opportunities for priority effects, whereby the order of arrival determines assembly processes and, ultimately, diversity patterns (Fukami, 2015; Vannette & Fukami, 2017). This is also evident during primary succession, such as on recently exposed substrates after deglaciation or newly formed terrain after a volcanic eruption. Primary succession is strongly influenced by the proximity of colonizers and their life-history characteristics (Tsuyuzaki & del Moral, 1995). For example, new substrates near intact vegetation will develop more quickly compared with isolated sites (Fuller & del Moral, 2003).

Importantly, how edaphic variation influences dispersal and the resulting diversity patterns is dependent on the dispersal ability of the species present (Holyoak et al., 2005; Leibold et al., 2004). Plant species found on edaphic islands often have longer-distance dispersal syndromes that allow them to disperse to and maintain populations in isolated edaphic outcrops (Spasojevic et al., 2014; Vandvik & Goldberg, 2006). However, in addition to the often patchy distribution of unusual soils across the landscape, the unique environmental conditions of unusual soils can also mediate how edaphic variation influences dispersal. For example, resource availability can constrain the availability and efficiency of different modes of dispersal (Flinn, Gouhier, Lechowicz, & Waterway, 2010; Ozinga et al., 2004; Willson, Rice, & Westoby, 1990). On unusual soils with low fertility, lower resource availability can lead to lower abundances of vertebrates, which can, in turn, lead to a lower prevalence of vertebrate dispersal in plants (Edwards, Dunlop, & Rodgerson, 2006; Hughes & Westoby, 1992). In addition, the open vegetation structure of many unusual soils can promote the efficiency of wind dispersal (Howe & Smallwood, 1982; Nathan et al., 2008). On newly formed substrates, wind-dispersed species are the most usual colonizers (Chang & HilleRisLambers, 2019; Chapin, Walker, Fastie, & Sharman, 1994; Karadimou et al., 2018). Furthermore, lower water availability can hinder the production of fleshy fruits dispersed by vertebrates (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008; Tabarelli, Vicente, & Barbosa, 2003). Lastly, edaphic variation can indirectly influence dispersal because dispersal syndromes can be functionally and/or phylogenetically non-independent of the traits that allow a species to persist on newly formed substrates or unusual soils. For example, Spasojevic et al. (2014) found that dispersal syndromes of plants on serpentine soils were not phylogenetically independent of the stress-tolerant functional traits that allow species to persist on this unusual soil type. Thus, dispersal syndromes can be indirectly constrained by the traits required to persist on newly

formed substrates or unusual soils (see “Niche selection” below), making it difficult to distinguish the direct causal relationship of edaphic variation on dispersal (Ronce, 2007; Spasojevic et al., 2014; Westoby, Leishman, & Lord, 1996).

By creating spatial variation in the environment, edaphic variation has the potential to influence dispersal and the resulting patterns of diversity strongly (Harrison, 2011). In some cases, such heterogeneity can increase diversity through spatial storage effects (Chesson, 2000), if patches are close enough in space to allow dispersal. For example, Russo, Porrs, and Tan (2007) found that demographic trade-offs sorted species into different habitats along an edaphic gradient and suggested that this sorting could facilitate species coexistence in a Bornean rainforest. In other cases, patches may be far enough apart, reducing connectivity among patches and contributing to speciation (as described in “Speciation” above), resulting in greater diversity over longer time-scales. In contrast, decreased connectivity can increase the probability of demographic stochasticity (see “Ecological drift” below), which can result in extinctions and a reduction in diversity.

2.3 | Ecological drift

Ecological drift is defined as changes in species relative abundances that cannot be predicted based on species identities or functional traits (Vellend, 2016; Vellend et al., 2014). Ecological drift is a key process in the unified neutral theory of biodiversity and biogeography (Hubbell, 2001), but is not synonymous with neutral theory because it does not include dispersal or speciation. Similar to neutral theory, however, ecological drift influences community dynamics and diversity patterns via stochastic births and deaths (Chase, 2007; Gilbert & Levine, 2017) and is the ecological analogue of genetic drift (Hubbell, 2001; Vellend, 2016; Vellend et al., 2014).

Although edaphic variation can influence diversity by creating spatial heterogeneity in the environment and influencing dispersal probabilities, the size and isolation of edaphic patches will also influence the relative importance of ecological drift. In general, species on smaller and more isolated edaphic patches (islands of unusual soil, in particular) will have higher probabilities of extinction, owing, in part, to lower recolonization from other similar habitat types (Aguilar, Quesada, Ashworth, Herrerias-Diego, & Lobo, 2008; MacArthur & Wilson, 1967), but also because of demographic stochasticity (Vellend et al., 2014). For example, Gil-López, Segarra-Moragues, and Ojeda (2017) found lower species richness and a stronger role of ecological drift in structuring plant communities on isolated sandstone habitat islands, and recent experiments and simulations have shown that smaller community size can increase the relative importance of ecological drift relative to niche selection (Gilbert & Levine, 2017; Ron, Fragman-Sapir, & Kadmon, 2018). Although the isolation and small size of edaphic islands can reduce population sizes and increase demographic stochasticity, the predominance of clonal reproduction in many edaphic endemic plant

species is one mechanism that might counteract the extinction of small populations by preserving genetic variation and mitigating the effects of demographic stochasticity (D'Amato, 1997; Schaal & Leverich, 1996).

The impact of edaphic variation on ecological drift has been less studied than speciation, dispersal or niche selection, and continued research on the impact of edaphic variation on ecological drift is needed. Although we know less about its impact, ecological drift has great potential to impact plant diversity patterns in edaphically heterogeneous landscapes where community size can vary dramatically. Although ecological drift is known to reduce local diversity via local extinction and to increase spatial variation at the landscape scale (beta diversity) (Gilbert & Levine, 2017), how and when edaphic variation increases or decreases ecological drift is not well known.

2.4 | Niche selection

Niche selection describes changes in species relative abundances attributable to abiotic and biotic conditions that give rise to deterministic differences in fitness between species (Vellend, 2016). In community assembly, this is often referred to as the abiotic and biotic filters and describes the deterministic drivers of diversity (Weiher et al., 2011). At its simplest, edaphic variation influences niche selection and diversity patterns by creating spatial heterogeneity, increasing opportunities for species sorting along environmental gradients (Amarasekare, 2003; Chase & Myers, 2011; Stein, 2015; Stein, Gerstner, & Kreft, 2014; Whittaker, 1960). Such spatial variation in edaphic properties also selects for different traits in different local environments within a region, thereby increasing functional diversity in regions with greater environmental heterogeneity (Harrison et al., 2006). How spatial variation in soil properties changes with soil development is unclear (Laliberté et al., 2013), although one hypothesis is that more productive ecosystems show lower spatial heterogeneity (Tilman & Pacala, 1993). Over longer time-scales, edaphic heterogeneity can create microrefugia from climatic variability (see “Climate change” below). For example, the rugged terrain, climatic stability and complexity of soils and microclimates allowed the Klamath-Siskiyou region of Oregon and California (USA) to serve as a refuge from past climatic changes for species and natural communities (Coleman & Kruckeberg, 1999; Sawyer, 2007; Whittaker, 1960).

Edaphic specialists are under different selection regimens compared with non-specialists because edaphic specialists are generally subjected to increased metal concentrations, lower water availability, lower nutrient availability, higher light levels and poor soil structure (Harrison & Rajakaruna, 2011; Kruckeberg, 2004). As a result, many edaphic specialists have a unique suite of stress-tolerance traits that allow them to persist in less favourable environments (Anacker & Harrison, 2011; Fernandez-Going, Anacker, & Harrison, 2012; Spasojevic et al., 2014). Niche selection for tolerance to edaphic extremes (abiotic constraints) has been hypothesized to

incur a cost to edaphic specialists in that they are poorer competitors (Kruckeberg, 1954), suggesting that soils can also influence biotic interactions. Indeed, the traits that allow species to be successful on unusual soils are not always the same traits that make for strong competitors (Anacker, 2014; Bastida, Rey, & Alcántara, 2015; Milla, Escudero, & Iriondo, 2011; Moore, Merges, & Kadereit, 2013). Moreover, experimental studies have found that some unusual soil endemics can be successful on “regular” soils, but only when neighbours are removed (Jurjavcic, Harrison, & Wolf, 2002; Proctor & Woodell, 1975). Furthermore, biotic interactions, such as facilitation, are especially important in maintaining diversity in unusual soils, particularly in those environments considered harsh or extreme. For example, Freestone (2006) found that the removal of a neighbouring moss species reduced the emergence of a serpentine specialist plant species (*Delphinium uliginosum* Curran.), suggesting an important role for facilitation. In harsh environments, such as those caused by unusual soils, facilitation should be particularly common (Bertness & Callaway, 1994), as seen in alpine environments (Callaway et al., 2002). Over long periods of time, positive interactions among plants in harsh environments can ameliorate the environmental stress of unusual edaphic formations, increasing the diversity of plants and other taxa.

In addition to interactions among plants, multi-trophic interactions are also influenced by edaphic properties (Strauss & Boyd, 2011; Van Nuland et al., 2016). Resource limitation on unusual soils can increase physiological costs associated with herbivore damage. The resulting barren and open landscapes can make plants more obvious to herbivores (Strauss & Boyd, 2011), and the resulting plant–herbivore interactions are central to edaphic specialization (Fine, Mesones, & Coley, 2004; Lau, McCall, Davies, McKay, & Wright, 2008; Van Zandt, 2007). Moreover, the increased herbivore pressure owing to increased noticeability on rock outcrops often leads to increased investment in defensive strategies (Strauss & Cacho, 2013), whose high costs can result in additional trade-offs in competitive ability (Fine et al., 2006), further restricting plants to unusual soils. On the contrary, the pathogen refuge hypothesis (Kruckeberg, 1992; Springer, 2007) suggests that plants experience lower pathogen pressure in edaphically harsh environments, owing to lower transmission rates in open landscapes (Thrall, Hochberg, Burdon, & Bever, 2007). Lastly, owing to resource limitation on unusual soils, belowground interactions with symbiotic mycorrhizal fungi are important for many edaphic specialist plant species. For example, the vast majority of serpentine plants are associated with arbuscular mycorrhizal fungi, and this often includes plants belonging to families that are non-mycorrhizal in non-serpentine soils (Hopkins, 1987). All these trophic interactions scale up to influence regional-scale patterns of biodiversity. If species segregate across edaphic properties, natural enemies specialized to them will also show spatial sorting across environments, increasing regional diversity across trophic levels.

To conclude, edaphic properties have strong and varied effects on niche selection, and multiple processes act within and among trophic levels to impact diversity patterns. Within a trophic level, niche

selection will result in species sorting across habitats and alter the relative importance of biotic interactions. Facilitation, for example, can help species to persist on unusual soils, but competitive ability can be reduced as a cost of tolerating unusual soils. Likewise, across trophic levels, both antagonistic and mutualistic interactions influence diversity patterns where herbivore pressure can be greater on unusual soils, but reduced pathogen load and increased prevalence of symbioses can benefit many species. Further research is still needed to generalize the nature of these complex interactions and how they vary across edaphic gradients.

3 | CLIMATE CHANGE AND THE EDAPHIC CONTROL OF PLANT DIVERSITY

Modelling approaches for predicting the impact of climate change on plant diversity and distribution patterns have largely focused on predicting future habitat for individual species based on climate envelope models. Although climate envelope models are a useful first approximation of the potential impact of climate change, they have received criticism for ignoring other important factors that determine a species distribution, particularly topography and edaphic variation (Anderson & Ferree, 2010; Araújo & Guisan, 2006; Berry, Dawson, Harrison, Pearson, & Butt, 2003; Bertrand, Perez, & Gégout, 2012; Dobrowski, 2011; Dubuis et al., 2013; Figueiredo et al., 2018; Hjort et al., 2012; Pearson & Dawson, 2003). Including edaphic variation in distribution models is obvious for soil endemics (Damschen et al., 2012) where a required soil substrate might be entirely absent from projected climate envelopes, as shown for limestone specialists in the U.K. (Berry et al., 2003). Climate envelope models would also have poor predictive power in regions of high edaphic heterogeneity, such as in many biodiversity hotspots around the world (Myers et al., 2000), where microclimates and edaphic variables interact strongly. The importance of dispersal and biotic interactions will be for predicting the outcome of climate

change on species distributions in edaphically diverse regions (Record et al., 2018).

The mosaic of microhabitats in regions of edaphic complexity, such as the granite outcrops of south-western Australia (Hopper & Gioia, 2004), have provided refugia during past climatic events and will continue to be important refugia under future climate change (Keppel et al., 2018). Climate relicts are more common than previously realized and are considered important components of local and regional diversity, maintained by the thermoregulation of topographical and other terrain effects (Hampe & Jump, 2011). Patterns of Quaternary refugia were predicted by bedrock type in the Alps, for example, where bedrock predicted both past and present-day species distributions (Alvarez et al., 2009; Schönswetter, Stehlik, Holderegger, & Tribsch, 2005). Edaphically complex regions are spatially heterogeneous, creating microhabitats that differ in soil properties such as acidity, drainage and erodibility and thus the availability of water and soil nutrients. The microhabitat variation of edaphically heterogeneous regions probably increases the chances of survival for organisms that differ in their environmental requirements (Virah-Sawmy, Gillson, & Willis, 2009) because of an increased probability that a suitable environment will occur (Keppel et al., 2015). Indeed, habitat specialization (Svenning, 1999; Tuomisto et al., 1995), species survivorship (Ohlemüller et al., 2008) and habitat quality (Weiss, Murphy, & White, 1988) are all linked to microhabitat variation. Over longer time-scales, microhabitats can persist as microrefugia, and past microrefugia in edaphically heterogeneous regions lead to high rates of endemism and species diversity in these regions (e.g., Pepper, Doughty, & Keogh, 2013; Potzger, 1945). For this reason, geodiversity has been incorporated into conservation plans ("Conserving Nature's Stage") as a surrogate for both past and future biodiversity (Brazier, Bruneau, Gordon, & Rennie, 2012; Faith & Walker, 1996; Gill et al., 2015; Hjort et al., 2015; Hunter, Jacobson, & Webb, 1988).

Given the apparent pervasiveness of edaphic differentiation, a key research priority is to determine whether edaphically

TABLE 1 Major knowledge gaps linking edaphic variation to patterns of plant diversity and distributions, with examples of important assembly processes and exemplary research

	Knowledge gaps	Assembly processes	Examples
1	Plant diversity and productivity of unusual soils in tropical latitudes	Frequency of local adaptation to distinct soil types in tropical climates	Cuba: Oviedo et al. (2014); Puerto Rico: Medina, Cuevas, Figueroa, and Lugo (1994); Dominican Republic: Cano, Cano-Ortiz, Del Río, Veloz Ramirez, and Esteban Ruiz (2014); Brazil: Fine et al. (2005)
2	Biological realism in species distribution models	Effects of patch size and connectivity on species dispersal probabilities	Damschen et al. (2012); Record et al. (2018)
3	Mechanisms underlying scaling relationships between species diversity, functional trait diversity and edaphic variation	The contribution of phenotypic plasticity versus local adaptation in producing diversity gradients and mediating responses to global change	Botero et al. (2015); De Jong (2005); Fazlioglu et al. (2017); Ghalambor et al. (2007)
4	Linking the spatial arrangement of edaphic variation and ecological drift	The influence of dispersal and ecological drift on community size and population persistence and extinction rates	Byrne et al. (2019); Gil-López et al. (2017)

differentiated plant communities are especially vulnerable or resistant to climate change (*sensu* Damschen et al., 2012). On the one hand, the spatial isolation that characterizes edaphic outcrops can act as a strong barrier for dispersal to more suitable climates (Spasojevic et al., 2014). Dispersal limitation can be pervasive in areas of high edaphic heterogeneity where habitat suitability is patchily distributed or occurs in narrow bands within a larger geological mosaic (see “*Dispersal*” above). On the other hand, edaphically differentiated plant communities are characterized by adaptations to stresses, such as drought and nutrient limitation (see “*Niche selection*” above), which can buffer these communities from the effects of climate change. However, these adaptations (such as small plant stature and low specific leaf area) are associated with slow growth, making it difficult to quantify responses to climate change over short time-scales, at least for long-lived plants. Indeed, the best evidence for climate change responses on edaphically unique substrates comes from grasslands (e.g., Grime et al., 2008; Harrison, Damschen, Fernandez-Going, Eskelinen, & Copeland, 2015). Studies relating climate change to serpentine flora note the increased temporal stability relative to adjacent soil types (Damschen et al., 2012; Grime et al., 2008). Additional evidence for the stability of unusual edaphic communities over longer time-scales has been observed based on a palaeoecological comparison of unusual and adjacent soils using pollen sequences from California lakes (Briles, Whitlock, Bartlein, & Higuera, 2008). Despite the potential for stability on unusual soils, climate change can alter soil structure and stability (Holzinger, Hülber, Camenisch, & Grabherr, 2008; Karmakar, Das, Dutta, & Rakshit, 2016), nutrient availability via atmospheric deposition (Weiss, 1999), and competitive interactions (Kruckeberg, 1984; Safford et al., 2005). Moreover, other human activities, such as increased grazing, habitat fragmentation and altered fire regimens, will contribute to the loss of specialized floras and the biota that depend on these unique edaphic habitats.

4 | KNOWLEDGE GAPS

It is clear that edaphic properties and climate interact to determine plant diversity patterns across large spatio-temporal scales. Nevertheless, discussions relating climatic and edaphic variation are predominantly concentrated in temperate latitudes. The serpentine outcrops of Cuba (Oviedo et al., 2014) and New Caledonia have the richest known serpentine flora in the world, but other tropical serpentine or edaphic habitats are much less studied (Table 1; knowledge gap 1). Tropical plant diversity in edaphic habitats can differ fundamentally in speciation rates, niche selection, ecological drift and dispersal owing to geological processes, the time available for colonization, the spatial distribution of edaphic outcrops or interactions with climate. For example, the tall gallery forests that develop on serpentine outcrops in Puerto Rico suggest that soil nutrients are not a limiting factor for plant growth or biomass (Weaver, 1979), and

other tropical gallery forests that develop on unusual, low-fertility soils point to important feedbacks between plants, soil nutrient cycling and climate. Furthermore, whereas fire, drought and over-grazing are prominent disturbance factors in edaphic habitats of the temperate zone (Safford & Harrison, 2001, 2004), prominent disturbance factors in tropical latitudes include earthquakes and storms, often resulting in landslides. Landslides remove soil, vegetation and rock, exposing substrates that differ in composition and creating patches of bare ground varying in size (Restrepo & Alvarez, 2006). The resulting variability in patch size and subsequent edaphic composition might help to explain the high levels of plant diversity found in tropical and subtropical mountains (Gentry, 1992), but this is not broadly studied. Finally, there is growing evidence that cross-kingdom interactions, such as herbivory (Fine et al., 2004) and arbuscular mycorrhizal fungi (Casper et al., 2008), are key features of edaphic adaptation that might be especially important in tropical latitudes. There are too few studies to make broad generalizations across latitude (Strauss & Boyd, 2011) relating how edaphic and climatic factors jointly influence patterns of plant diversity.

One approach for overcoming the inability to make broad generalization across latitude is the use of biologically realistic species distribution models. The need to include both climatic and edaphic factors is increasingly recognized as part of the next generation of species distribution models (Table 1; knowledge gap 2). The public accessibility of global climate (e.g., WorldClim; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; CHELSA; Karger et al., 2017) and soil data (e.g., Harmonised World Soil Database; Nachtergaele et al., 2010) makes it possible to disentangle climatic and edaphic effects on diversity patterns (see Bailey et al., 2018; Parks & Mulligan, 2010; Schrodt et al., 2019). In addition, the application of remote sensing and satellite-derived products (e.g., Higgins et al., 2011; Zarnetske et al., 2019) facilitates the inclusion of other geological data into predominantly climate-based models. Doing so will form a new chapter in our understanding of macroecological patterns of plant distributions and diversity and highlight the role of edaphic factors in shaping the biodiversity gradients of the world.

One mechanism by which edaphic variation can shape plant diversity gradients is through phenotypic plasticity and local adaptation. Yet, the contribution of phenotypic plasticity versus local adaptation to diversity gradients in edaphically complex landscapes is largely unknown (Table 1; knowledge gap 3). Phenotypic plasticity influences species responses to environmental change and, as a result, is important in determining species distributions (Gratani, 2014). Phenotypic plasticity can also influence natural selection and, thus, patterns of diversification among populations and species (Scheiner, 1998; Sultan, 2004). Likewise, local adaptation across edaphic gradients can increase diversity and facilitate coexistence (Lankau, 2011). Arguably, environmental predictability and the scale of environmental variation determine the value of phenotypic plasticity versus adaptive strategies such as bet-hedging (Botero, Weissing, Wright, & Rubenstein, 2015). If this is true, then the spatial arrangement of edaphic variation might lead to predictable patterns

of phenotypic plasticity and local adaptation. A renewed appreciation for the extent and consequences of intraspecific trait variation in community assembly research (e.g., Bolnick et al., 2011; Violle et al., 2012) can help to address this knowledge gap. Intraspecific trait variation is a result of local adaptation and/or phenotypic plasticity and influences the outcome of community assembly processes (e.g., speciation, drift, dispersal and selection) (de Bello et al., 2011; Hulshof et al., 2013; Laughlin, Joshi, van Bodegom, Bastow, & Fulé, 2012; Lepš, de Bello, Šmilauer, & Doležal, 2011). The extent to which edaphic variation promotes diversity and intraspecific trait variation (and the extent to which that trait variation is plastic or adaptive) provides a useful framework for understanding adaptation to changing environments (i.e., Botero et al., 2015), especially under rapid rates of climate change. Preserving areas where intraspecific trait variation is high (such as in edaphically heterogeneous areas) might help to buffer populations against future environmental extremes attributable to changes in climate or land use (Gratani, 2014).

Finally, community size can play a key role in influencing the relative role of ecological drift relative to other assembly processes (Gilbert & Levine, 2017; Ron et al., 2018), and edaphic variation has the potential to influence community size (e.g., communities restricted to small patches of unusual soils will be smaller). Thus, ecological drift has the potential to play a greater role in edaphically complex landscapes. For example, edaphic specialists restricted to small, isolated fragments are highly susceptible to demographic stochasticity, genetic depletion and, ultimately, local extinction (Aguilar et al., 2008; Gil-López et al., 2017). However, in regions with a high degree of edaphic variation, it is still unclear how the spatial arrangement and connectivity of edaphic islands influences ecological drift at the community level and demographic stochasticity at the population level (Table 1; knowledge gap 4). Communities and/or species on small patches of unusual soils that are, in theory, more susceptible to ecological drift might be rescued by dispersal (source-sink dynamics; Amarasekare et al., 2004; Anderson & Geber, 2010; Mouquet & Loreau, 2003). Alternatively, clonal reproduction might counteract the extinction of small populations by preserving genetic variation and mitigating the effects of demographic stochasticity (D'Amato, 1997; Schaal & Leverich, 1996). Regardless, the high inherent vulnerability of edaphically rare, specialized or endemic species demonstrates an urgent need for conservation of edaphically complex landscapes. Owing to their unique spatial arrangement and natural variation in community and population size, edaphically complex landscapes can provide a powerful natural experiment to gain a better understanding of the importance of ecological drift. Moreover, understanding the strength of ecological drift on unusual soils is crucial for accurate prediction of how these communities will respond to climate change.

5 | CONCLUSIONS

Quantification of the relationship between edaphic variation and plant diversity is necessary for predicting responses to future

environmental change. Our review highlights evidence that edaphic variation is a fundamental driver of diversity gradients, yet its generality and predictive ability has yet to be explored fully. We outline four key processes (speciation, dispersal, ecological drift and niche selection) by which edaphic properties can give rise to diversity gradients. Edaphic and, more broadly, geological heterogeneity provides novel opportunities for speciation, which will influence the regional species pools from which local communities assemble. The spatial distribution of edaphic variation across the landscape will influence dispersal, increasing opportunities for source-sink dynamics and priority effects, but the influence of edaphic variation on dispersal will be mediated by the distance between patches, dispersal syndromes and the edaphic environment itself, which might favour certain forms of dispersal over others. The effects of ecological drift on regional diversity and species turnover in edaphically complex regions might also depend on dispersal probabilities, the spatial arrangement and size of patches in a landscape and the modes of reproduction. At its simplest, niche selection can increase diversity through increased endemism on unusual substrates. However, its impact on biotic interactions, both within and among trophic levels, is poorly understood.

Edaphic variation provides an ideal platform for studying the relative importance of assembly mechanisms that drive diversity patterns and represents an untapped resource for parsing out the impact of multiple interacting factors. Nevertheless, our understanding of the edaphic control of plant diversity is nascent. The four knowledge gaps outlined here provide a roadmap for expanding work in tropical latitudes, for improving modelling capabilities, for better linking of species diversity, functional trait diversity and edaphic variation, and for quantifying the ubiquity of ecological drift across edaphically complex areas. Most of our understanding of the edaphic control of plant diversity comes from temperate latitudes, which underscores a pressing need to build collaborative relationships with scientists from tropical countries (Ramirez et al., 2017; Stocks, Seales, Paniagua, Maehr, & Bruna, 2008). Until then, broad generalizations of the role of edaphic variation will be incomplete. Efforts to build more accurate species distribution models using both edaphic and climatic predictors are gaining momentum, and we hope to see their application to entire community assemblages to gain a better understanding of how climate change might impact geodiverse and edaphically unique regions. Other modelling approaches should emphasize the spatial and temporal scaling relationships between edaphic variation and intraspecific trait variation. Patterns of functional trait variation across environments appear species specific and site dependent, and these idiosyncrasies point to the possibility of modulation by environmental heterogeneity driven by climatic and edaphic interactions. Edaphic heterogeneity across spatial and temporal scales and plant functional strategies might also help to elucidate the role of ecological drift, particularly as edaphic islands or geodiverse regions experience increased global change pressures. By highlighting the linkages between edaphic variation and plant community assembly processes, we hope that our review guides future work

to develop and evaluate mechanistic models of diversity and predict better how plant diversity responds to changing environmental conditions.

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DATA AVAILABILITY STATEMENT

Global distributions of serpentine outcrops are archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.sqv9s4n1r>). Global biodiversity hotspot GIS data are available at <https://databasin.org/datasets/23fb5da1586141109fa6f8d45de0a260> (Conservation Synthesis, Center for Applied Biodiversity Science at Conservation International 2011).

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