A systematic review of transplant experiments in lichens and bryophytes

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Abstract. Transplant studies have long been a cornerstone of experimental ecology. Lichens and bryophytes have several useful characteristics for transplantation: they are small, easily transported, and highly responsive to environmental gradients. Here we conduct a systematic review to synthesise lichen and bryophyte transplant studies up until March 2020 (*N*=454). A great majority of studies (67%) used lichen and bryophyte transplants as biosensors of airborne pollutants. Other research themes such as forest management and biotic interactions were associated with comparably modest bodies of work. A total of 247 lichen and bryophyte species had been used in transplant studies, but four species predominated: *Hypogymnia physodes*, *Pseudevernia furfuracea*, *Evernia prunastri* and *Lobaria pulmonaria*. Liverworts were only transplanted in 4% of studies, and most studies focused on epiphytic (69%) or terricolous species (31%). A small group of studies (*N*=15) used whole-community transplants with areas ranging from 25–250,000 cm^2. Apart from pollution research, studies centered on assisted colonization and simulated climate change appear to be increasing most rapidly in time. There were several recurrent lines of investigation within the included literature (e.g., edge effects, colonization of young forests, climate change effects and local adaptation) and we synthesise the key results. We recommend that future research address underrepresented taxa (e.g., liverworts, biological soil crusts) and geographic gaps, namely Australia and Africa.

Keywords. Biomonitoring, climate change, cryptogam, edge effects, experimental ecology, local adaptation, non-vascular, plasticity, pollution, transplantation.

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For several decades now, a tension has existed between experimental and observational research in ecology (McGill 2019). Experiments have long been seen as the gold standard in ecology, since well-designed experiments can separate causation from correlation and build a much stronger inferential framework. However, it has also been widely recognised that experimental studies cannot match the spatial and temporal scales of many, if not most, macroecological processes (Benedetti-Cecchi et al. 2018; Blackburn 2004; Brown 1999). In some cases, limitations to the temporal extent can be somewhat compensated by spatial surrogates (Fukami & Wardle 2005), but this limitation is profound and insurmountable for many questions. The fact that observations are the only available data for many questions has spawned a new generation of methods for using these data such as species distribution modelling (SDM), which is becoming increasingly common and powerful in the age of "big data" (Wüest et al. 2020). Nonetheless, the tension between experiments and observations has not disappeared and, if anything, the need for more experiments to inform observations has continued to grow (Alexander et al. 2016).

Transplant experiments, where individuals or communities are moved to locations with differing environmental conditions, have a long history in experimental ecology (Nooten & Hughes 2017). Often transplants are arrayed along a gradient of interest, such as climate, or pollution with increasing distance from a point source. Climate gradients,

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typically temperature and precipitation, are especially insightful because they can be used as a space-for-time substitution to predict the future responses of a transplanted species to climate change (Nooten & Hughes 2017). One prevailing line of investigation has been the use of "over-the-edge" transplants, where species are moved beyond their geographic range to disentangle the various abiotic and biotic constraints on their distribution (Hargreaves et al. 2014; Lee-Yaw et al. 2016). Another class of transplant experiment aims to assist the dispersal of a species, either to facilitate a range shift into newly suitable habitat (assisted migration; Loss et al. 2011) or to promote the recolonization of a disturbed area (Smith 2014).

While they are less common than experiments with individuals, whole-community transplants have the advantage that they allow localized biotic interactions, including those with microbes, to continue but in altered conditions. The manipulated condition can be biotic, such as grazing regime (Saccone et al. 2014), but in most cases relates to the macroclimate (Alexander et al. 2015; Meineri et al. 2020; Tomiolo et al. 2020). One of the main findings to emerge from these studies is that communities on the retreating edge of a shifting climate exhibit poor resistance to novel competitors (Alexander et al. 2015; Meineri et al. 2020). Alexander et al. (2016) make a compelling argument that many of the interactions among species under future climate change will be novel, and therefore an experimental approach with whole community transplants is crucial to inform our predictions of climate responses given that observational extrapolations are limited to known phenomena.

Lichens and bryophytes are highly amenable to transplantation because they are relatively small and easily moved. There are virtually no reports of non-vascular plants experiencing "transplant shock" (Close et al. 2005), unless they are transplanted to different microsite conditions (Cole et al. 2010). Additionally, lichens and bryophytes respond strongly to climate and pollution gradients, largely due to 1) their inability to regulate water loss (poikilohydry), 2) photosynthesis being dependent on hydration, 3) their reliance on atmospheric nutrient deposition and 4) their capacity to accumulate heavy metals and other airborne contaminants (Garty 2001; Green & Lange 1995; Zotz & Bader 2009). Epiphytes, which constitute 60–80 % of non-vascular species in tropical systems and 10–20 % in temperate systems (Zotz & Bader 2009), are a special case because their association with woody plants also makes them susceptible to forestry practises, the impacts of which have been the subject of numerous transplant studies (e.g., Stevenson & Coxson 2008; Stewart & Mallik 2006). Lichens and bryophytes are not only a convenient model system, but they also have considerable functional importance that merits investigation and conservation, including their roles as primary producers, nutrient cyclers, a food source and regulators of soil processes (Elbert et al. 2012; Mallen-Cooper et al. 2020; Storeheier et al. 2002).

In this systematic review, our main aim was to synthesize the broad range of transplant experiments using lichens and bryophytes. In doing so, we identify geographic areas where research has been prolific or noticeably absent, as well as the relative output of different research subfields. By identifying gaps and opportunities for future research, we hope to point the way forward for a new generation of experimental ecology using non-vascular cryptogams. Transplant experiments across a wide variety of climatic and ecological systems will be critical to our understanding of heterogeneous phenomena such as climate change and its effects on biota.

METHODS

We searched the Web of Science for all terrestrial studies, up until March 2020, of lichen or bryophyte transplantations using the search terms *(lichen OR moss OR bryophyte OR liverwort OR biocrust OR cryptogam) AND (transplant OR translocation)*. The search returned 977 records, of which those that were not peer-reviewed (*N*=42) were immediately removed. Records were included if the transplanted organism was a lichen or bryophyte inhabiting a terrestrial system (including wetlands). Duplicates (*N*=10), non-primary studies (*N*=19), and studies involving cultivated transplants (*N*=10) were excluded, as were studies that only used litter (*N*=6) or devitalized (*N*=9) material. It has been acknowledged that devitalised moss is generally more effective and less variable in the absorption of pollutants than living moss (Ares et al. 2012), yet our search only returned 11 transplant studies using devitalizing treatments. In total, 454 studies met the criteria for inclusion.

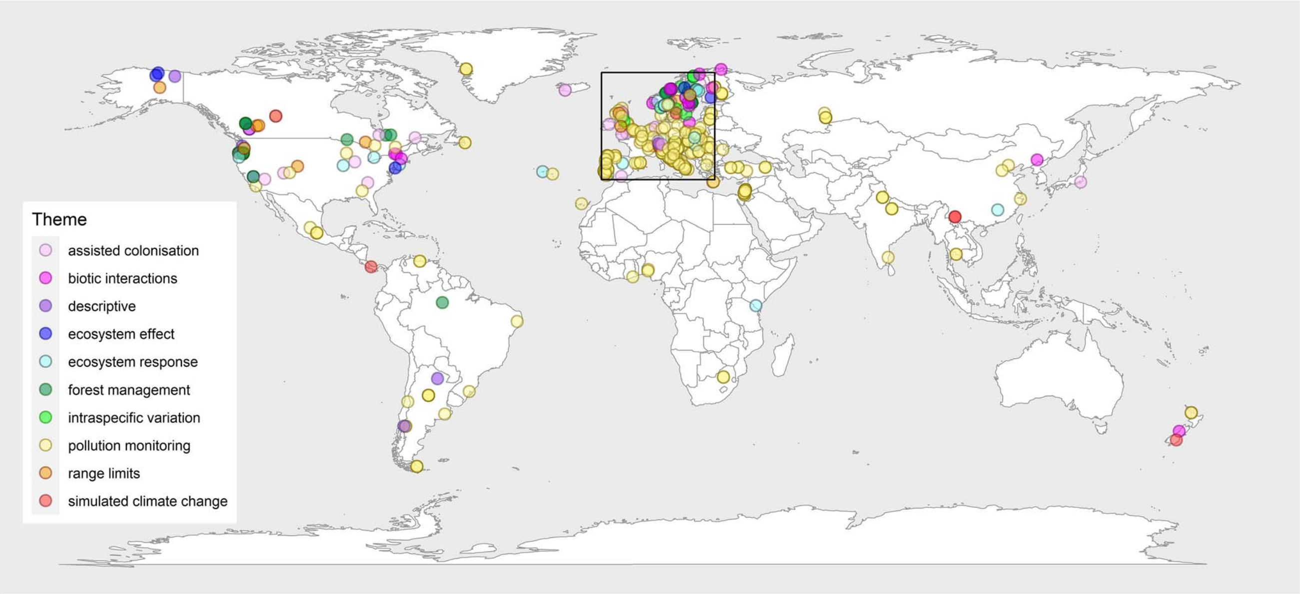

Figure 1. Global distribution of transplant studies, colored by research theme (black square indicates the extent of Supplementary Figure S2).

Studies were categorized into ten overarching research themes. *Assisted colonization* referred to any study where organisms were transplanted into an uncolonised area for the purposes of conservation or restoration. Studies that explored competition, grazing effects and other biotic relationships were classified as *biotic interactions*. Some works were purely *descriptive*, and documented, for example, growth patterns or rates (e.g., Rolstad & Rolstad 2008); in these studies, transplantation was typically used to standardize environmental conditions, that is, establish a common garden. Those studies that transplanted organisms to examine their responses to manipulated abiotic conditions or subsequent effects on ecosystem attributes were grouped into *ecosystem response* and *ecosystem effect* accordingly. However, responses to anthropogenic disturbances were categorised separately under the themes *forest management* and *pollution monitoring*. Pollution monitoring also encompassed a vast array of studies that deployed lichens and bryophytes as simple accumulators of heavy metals and other airborne pollutants. Studies investigating plasticity, acclimation and trait variation within a species were assigned as *intraspecific variation*, while studies that transplanted organisms beyond their known range boundaries were grouped into *range limits*. A particular subset of range limit studies can be differentiated into their own theme, *simulated climate change*, when organisms were intentionally transplanted as a space-for-time substitution.

Network analyses were conducted using the *bibliometrix* R package (Aria & Cuccurullo 2017). All data and code supporting the results have been deposited in the Open Science Framework, DOI 10.17605/OSF.IO/TH53J.

Results

Spatial distribution of studies. An overwhelming proportion of transplant studies were conducted in Europe, which largely reflects early recognition that lichens and bryophytes can be used as effective biosensors of pollution (**Fig. 1**; **Supplementary Table S1**; **Supplementary Fig. S1**). Pollution monitoring accounted for 70% of studies in Europe and 67% of studies globally. Particular cities were hotspots of pollution research, for example, Córdoba in central Argentina was the site of 17 distinct studies. Keyword associations show that pollution biomonitoring dominates the cryptogam transplant literature, while studies focusing more on ecology and physiology form their own cluster (**Fig. 3**).

To some extent, the high concentration of pollution studies in Italy, Portugal and Israel reflects the work of a few prolific research groups in those areas, namely led by Stefano Loppi (34 studies), Maria do Carmo Freitas (28 studies), Jacob Garty

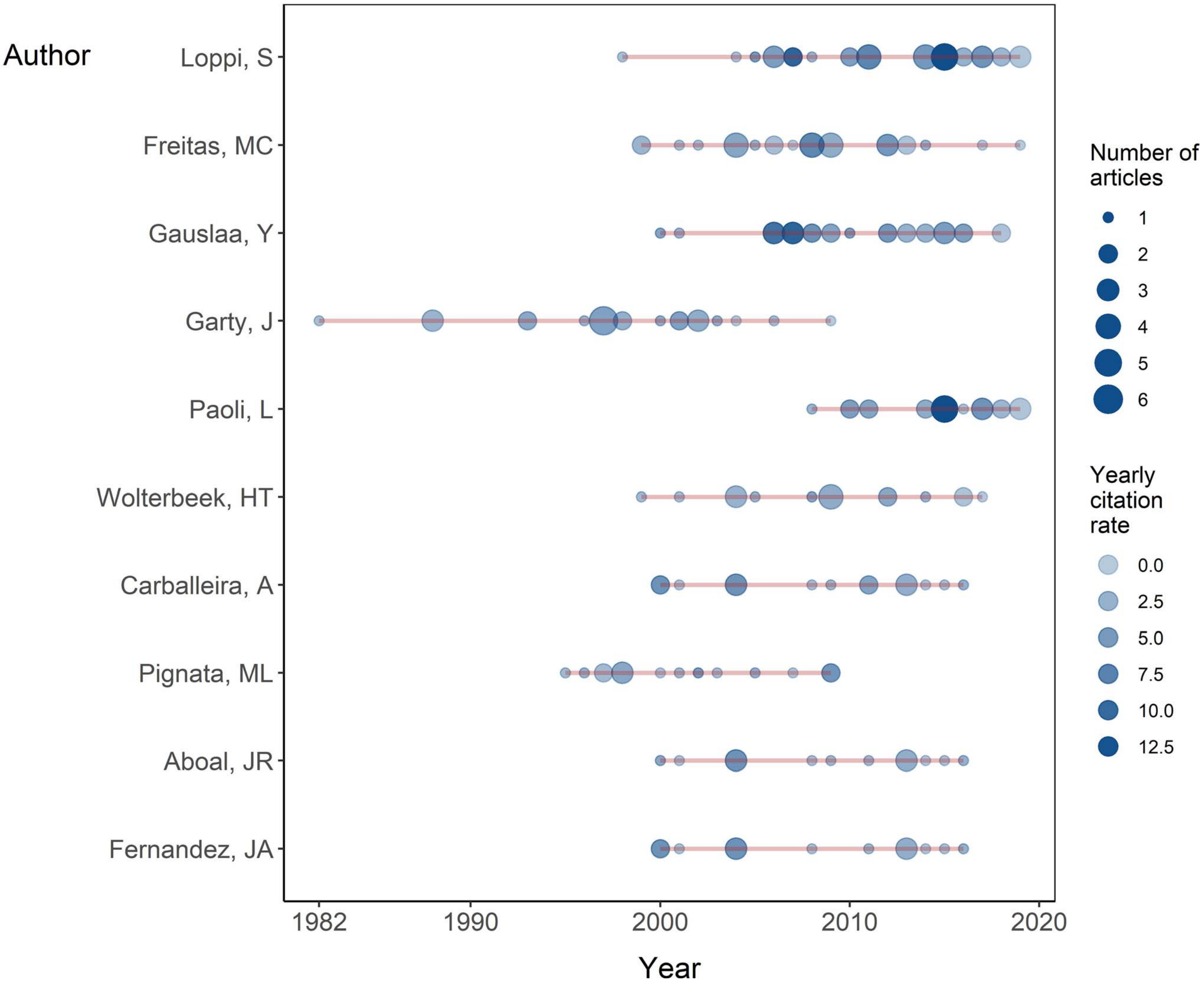

Figure 2. Production of the 10 most prolific authors of non-vascular transplant studies over time.

(25 studies) and Luca Paoli (21 studies; **Fig. 2**). In Norway, Yngvar Gauslaa (26 studies) is a key figure in fundamental research on epiphytic lichens. A collaboration network shows that authors most frequently collaborated within Europe, while authors affiliated with countries such as Chile, Ghana, Japan and Turkey tended to work alone or with co-authors from the same country (**Supplementary Fig. S3**).

Of the studies not relating to pollution, 92% were conducted in Europe (*N*=88) or North America (*N*=48). Studies assessing the impacts of forestry practices on lichens and bryophytes were quite evenly split among boreal (*N*=14) and temperate forests (*N*=10), with only one other study conducted in tropical Brazil (Zartman & Shaw 2006). More generally, the vast majority of studies were located in the temperate zone (81%), while tropical (4%), subtropical (13%), and polar (2%) studies were poorly represented.

Characteristics of study species. A total of 247 lichen or bryophyte taxa have been used in transplant experiments. The most frequently transplanted species was the epiphytic lichen *Hypogymnia physodes*, followed by *Pseudevernia furfuracea* and *Evernia prunastri* (**Table 1**). Outside the domain of pollution monitoring, *Lobaria pulmonaria* was the most common study species, with numerous studies documenting its growth under a range of environmental conditions (e.g., Renhorn et al. 1997) and its interactions with grazing gastropods and host trees (e.g., Asplund et al. 2018). Only 4% of studies

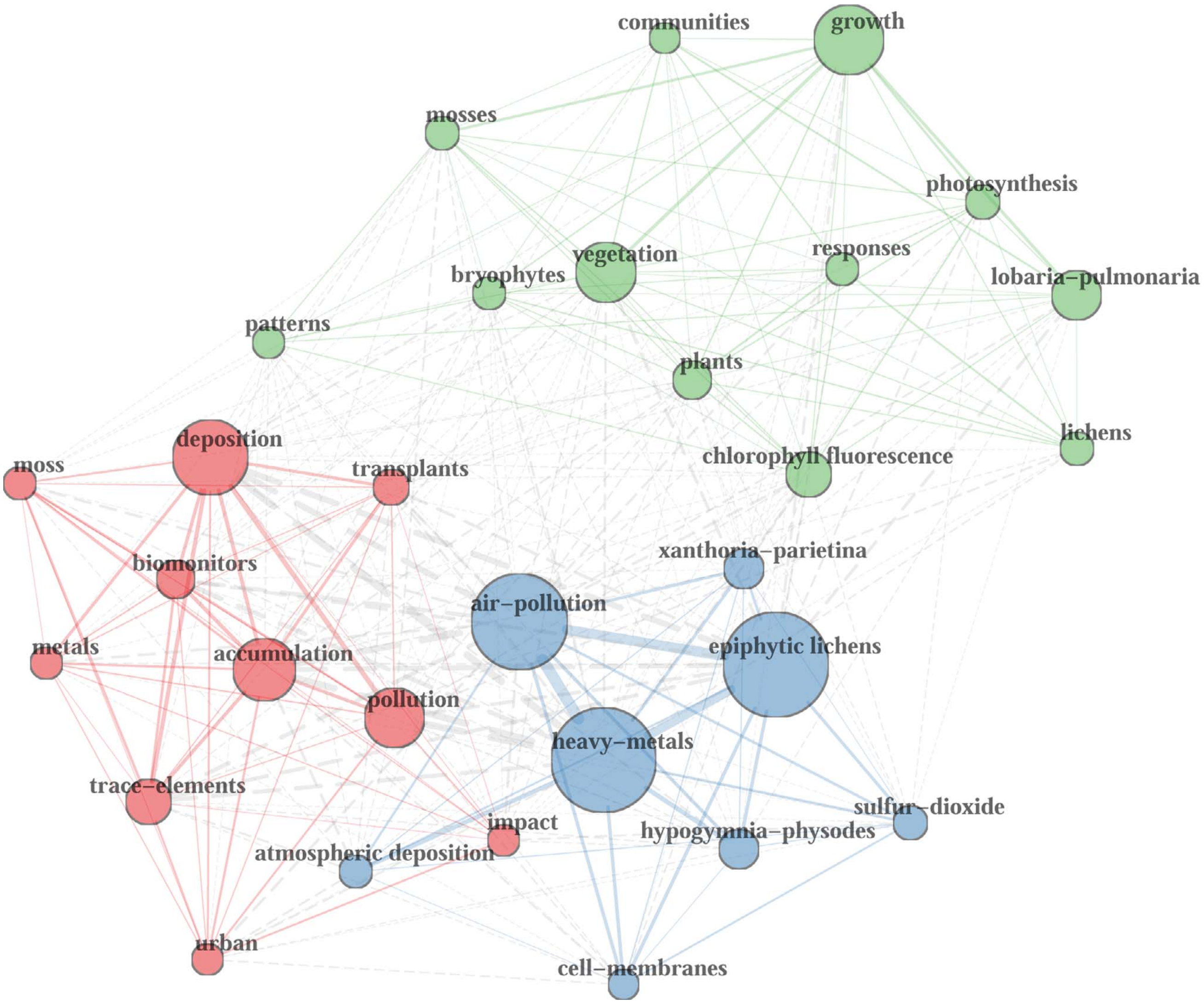

Figure 3. Network associations between the 30 most common keywords in non-vascular transplant studies (circle size is proportional to number of studies).

transplanted liverworts, while 29% and 75% of studies transplanted mosses and lichens respectively. Perhaps since liverworts rarely dominate large areas (but see Gudmundsdóttir & Andrésson 2019; Seppelt et al. 2016), they are not as easily collected, and their functional roles are underappreciated. Interestingly, biological soil crusts—terricolous communities of non-vascular cryptogams and microbes, sometimes called biocrusts, that are especially abundant in drylands (Belnap et al. 2016)—were the subject of only four transplant studies, in which single species were transplanted separately.

Epiphytic (69% of studies) and terricolous (31%) species dominated the transplant literature, while rock-dwelling (epilithic or saxicolous, 2%), wood-dwelling (epixylic, 1%), vagrant (unattached, 0.4%) and leaf-dwelling (epiphyllous or foliicolous, 0.2%) taxa were uncommon choices. Note that several studies used multiple species from different substrates. The ease by which epiphytic and terricolous species can be detached from their substrate likely explains their frequency in transplant studies. In some cases it is possible to scrape bryophytes off a rock surface or transplant a small rock with a lichen thallus attached (e.g., Garty et al. 2002), but saxicolous lichens growing on large rocks are unwieldy to transplant unless specialized equipment is used to detach a fragment of the substrate with the organism intact and attached (Fahselt

Table 1. Counts of studies with the 20 most commonly used cryptogam taxa, partitioned by research theme (L = lichen, M = moss).

	Division	Assisted colonization	Biotic interactions	Descriptive	Ecosystem effect	Ecosystem response	Forest management	Intraspecific variation	Pollution monitoring	Range limits	Simulated climate change
Hypogymnia physodes	L	1	1			1			43		
Pseudevernia furfuracea	L								42		1
Evernia prunastri	L					1			39		1
Lobaria pulmonaria	L		8	2		15	9		4	2	
Parmelia sulcata	L					1			29		
Pleurozium schreberi	M		1		1	2	1		17	2	
Pseudoscleropodium purum	M					1		1	20		
Ramalina lacera	L								21		
Flavoparmelia caperata	L					1			19		
Hylocomium sp.	M				2	1	2	1	6	1	
Hylocomium splendens	M				1	1	2	1	6	1	
Hypnum cupressiforme	M					1			10		
Lobaria scrobiculata	L		2			4	3				
Sphagnum fuscum	M	2	4						1	1	1
Xanthoria parietina	L					1			6	1	
Usnea longissima	L			1		1	3		2	1	
Rhytidiadelphus triquetrus	M		2			2	1		1	1	
Lobaria oregana	L					1	4			2	
Flavocetraria nivalis	L	1				2		1	3		
Hylocomiastrum umbratum	M		1			2	2	1			

1979). Despite being convenient to transport, vagrant species are relatively rare in most habitats, typically only found in sparse, low vegetation cover communities (Rosentreter 1993). Their relative rarity which might explain why they have not become model species for transplantation. Similarly, epiphylls tend to be restricted to evergreen tropical forests (Coley et al. 1993; Rogers & Barnes 1986) but have been shown to be highly responsive to microclimate and disturbance and may thus be good candidates for transplantation studies (Lücking 1997).

Temporal patterns. The earliest transplant experiment of non-vascular cryptogams in our search was, fittingly, a study describing a novel methodology for transplanting epiphytic lichens (Brodo 1961). Since this innovation, and the later development of the nylon bag technique (Goodman & Roberts 1971), there has been a marked proliferation of studies using lichens and bryophytes to detect airborne contaminants (**Fig. 2**). The basic principle of these studies is to transplant organisms into the vicinity of a pollution source, expose them for a period of time (typically several months) and compare the concentration of pollutants, such as heavy metals or polycyclic aromatic hydrocarbons, in the tissues of the transplants with control samples located at an "unpolluted" collection site. A small percentage of these studies (13%) solely measure physiological parameters that characterise the response of organisms to pollution, including chlorophyll fluorescence, cell membrane integrity and DNA damage (Cansaran-Duman et al. 2015; Sujetoviene & Galinyte 2016). Increasing far more rapidly in time are studies that only analyze pollutant levels (56%; **Supplementary Fig. S2**). There is also a suite of studies (31%) that assess both physiological responses and pollutants.

Studies of ecosystem responses and biotic interactions have been increasing steadily in time, albeit at a much slower rate than pollution biomonitoring studies. The two research themes that appear to be increasing most strikingly in recent times are assisted colonization and simulated climate change.

Whole community transplants. We found a total of 15 studies in which entire communities, comprising or including non-vascular cryptogams, were transplanted (**Supplementary Table S2**). In addition, there was one study in which the authors translocated an entire heathland that would have otherwise been destroyed by industrial development (Box et al. 2011). The most frequently transplanted communities were arctic-alpine vegetation and *Sphagnum*-dominated bogs. Only one study transplanted a non-terricolous community, a core of bark epiphytes (LeBlanc & Rao 1973). Communities were typically transplanted as rectangular monoliths including underlying soil, with areas ranging from 25–250,000 cm^2. Other studies used circular cores of vegetation and soil (Verville et al. 1998; Vitt et al. 2018).

Research synthesis. The technique discussed in this review has implications across different fields and includes studies that address a wide variety of research questions. As such, the results of the studies are diverse. Results relating to pollution monitoring have been discussed in several past reviews (Bargagli 2016; Garty 2001; Onianwa 2001). However, among the other research themes, there are certain lines of investigation that frequently recur and merit a brief synthesis.

Of the eight studies using transplants as a space-for-time simulation of climate change, seven reported declines in abundance or functioning with climate change (the remaining study was centered on soil processes). Declines were often driven by a warmer, drier climate that resulted in thermal stress and a reduced period of photosynthetic activity (Liu et al. 2018; Pirintsos et al. 2011), but in some systems, declines were primarily driven by competition with vascular plants (e.g., Breeuwer et al. 2010). One study, which transplanted bryophytes to drier climates, found that growth rate was initially reduced, but after 20 months, the surviving transplants had a similar growth rate to controls (Wagner et al. 2014). Although more research is required to understand this response, it suggests that the capacity to acclimate and compensate for reduced periods of photosynthesis exists within bryophyte populations and may be a critical buffer against the detrimental effects of climate change.

A common line of investigation among eight studies of intraspecific variation was the degree to which populations are locally adapted, and therefore do poorly in non-native climates, or exhibit plasticity, and are therefore able to acclimate. Traits relating to physiology, including rate of photosynthesis and epicortex thickness (a layer of secretions

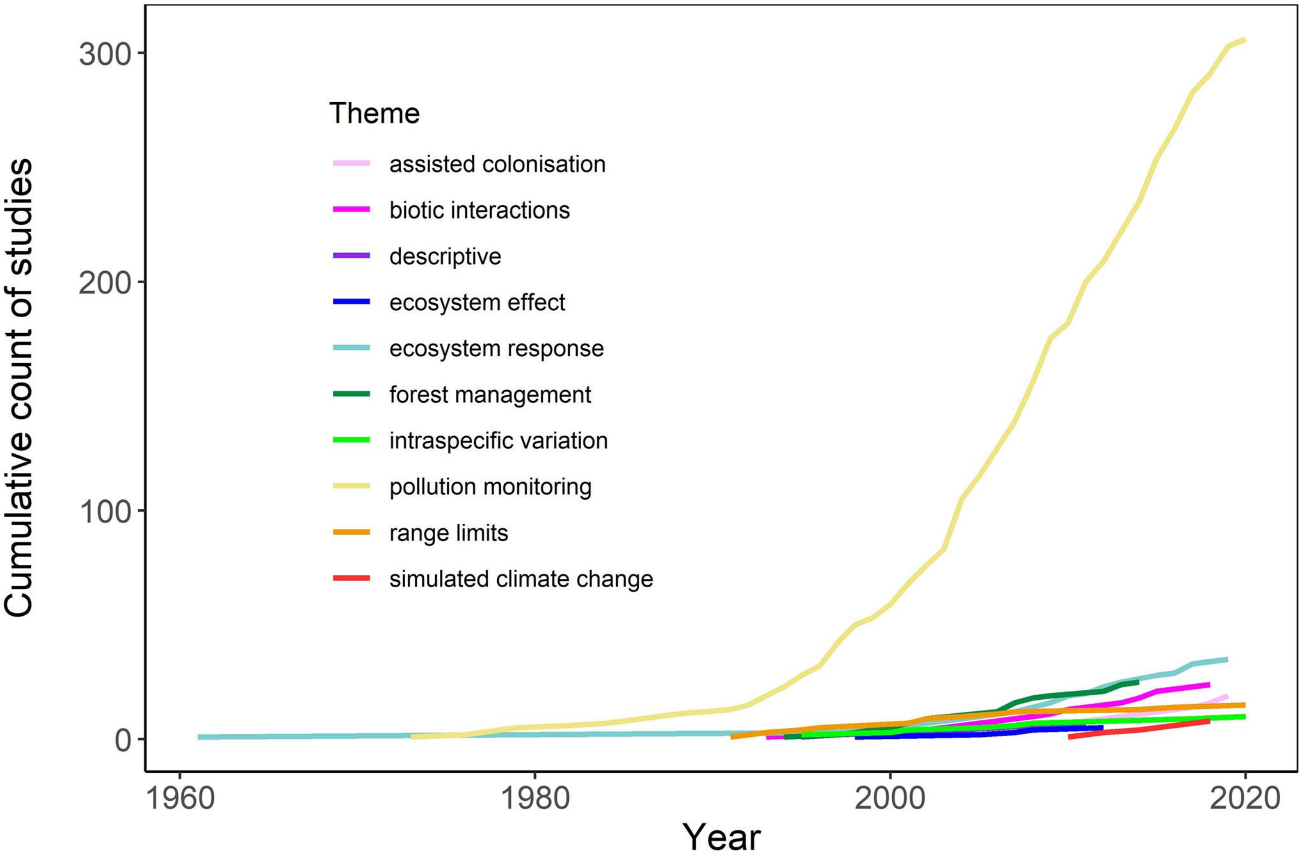

Figure 4. Accumulation of studies through time, colored by research theme.

on the surface of a lichen), were generally the most plastic, while morphological traits tended to be the least plastic (Schipperges et al. 1995; Sonesson et al. 2007). Two recent studies (Merinero et al. 2020; Williams et al. 2017) testing the performance of transplants in differing climates throughout their range both report that transplants performed poorly outside their native climate, indicating a degree of local adaptation and possibly an increased vulnerability to climate change.

There were two prevailing questions relating to the impacts of forestry:

1) What prevents old-growth associated cryptogams from establishing in young forests?
2) Do edge effects created by clear-cutting, including modified microclimate, affect cryptogam survival and vitality?

We briefly summarize the results of the reviewed papers on these below.

While it is often assumed that old-growth associated cryptogams perform optimally in those conditions (e.g., Lesica et al. 1991), seven transplant studies found that old-growth associated cryptogam species grew equivalently well in or better in young forest stands (e.g., Hilmo & Såstad 2001). There is therefore strong evidence that lichens and bryophytes associated with old-growth forests are limited by dispersal, establishment barriers such as competition, or poor propagule production. If dispersal is the limiting factor, assisted colonization and retaining old trees (i.e., propagule sources) may be viable management strategies (Hilmo & Såstad 2001). Establishment barriers are difficult to quantify in short-term studies and may be an underappreciated driver of lichen and bryophyte distributions. Simply finding DNA in a patch where no visible organisms grow (e.g., Werth et al. 2006) is insufficient evidence to conclude an establishment barrier, because it does not necessarily represent a viable organism or symbiosis.

Clear-cutting modifies the microclimate conditions of the bordering forest edge by increasing light availability, temperature extremes, wind speeds, weather exposure and often evaporative demand (Chen et al. 1995). Some aspects of the altered microclimate may benefit cryptogams while other aspects are thought to be detrimental. For example, increased light exposure is thought to be beneficial (up to a point), but there is also evidence that cryptogam species close to forest edges experience greater attrition due to storm exposure (Keon & Muir 2002). Lichens and bryophytes are known to be highly sensitive to microsite conditions, with assisted colonization studies reporting that factors such as sun exposure (Cole et al. 2010), microtopographical aspect (Davidson et al. 2002), and water level (Robroek et al. 2009) were some of the main drivers of establishment success. One takeaway from this review is that it is useful to consider cryptogam species separately, as the results of nine forestry studies suggest that species vary in their sensitivity to edge effects. Some species, such as *Usnea longissima* and *Lobaria pulmonaria*, performed better at the forest edge (Coxson & Stevenson 2007; Jansson et al. 2009) while others, including *Lobaria retigera* and *Hylocomium splendens* performed substantially worse (Stevenson & Coxson 2008; Stewart & Mallik 2006). One study that reported no edge effects on growth and vitality was conducted in a system with only minor differences in humidity from interior to edge (Renhorn et al. 1997), while another study found strong growth reductions in the edge habitat driven by a high vapor pressure deficit (Stewart & Mallik 2006), so it may be that the strength of the humidity gradient plays a dominant role in cryptogam performance. There is also evidence that "soft" edges, created by variable retention harvesting, reduce negative effects on sensitive species (Stevenson & Coxson 2008).

CONCLUDING REMARKS

One characteristic that links most types of transplant experiments is that they can be used to inform observational data. Manipulations of climate, competition, grazing or anthropogenic disturbance (e.g. pollution and forestry) are valuable mechanistic tests of the factors that control species distributions. While it is not feasible to experimentally test all relevant dimensions controlling the distribution of a species, it may be possible to formally integrate some experimental information into an SDM framework (Benedetti-Cecchi et al. 2018; Brooker et al. 2018). A "mechanistic SDM" of this nature could be the partnership that reunites experimental and observational ecology, harnessing the strengths of both approaches in a single analysis.

While it is clear that a plurality of transplant experiments with lichens and bryophytes can be characterised as pollution research, a modest but growing body of work has been established for other research themes such as biotic interactions and forestry impacts. There are geographic gaps, such as Australia and northern Africa, which could benefit from the various uses of transplantation. Biocrusts were also conspicuously absent from whole community transplant studies despite being easy to manipulate (Castillo et al. 2008). The emerging trend of studies relating to assisted colonization and simulated climate change likely reflects an urgency among ecologists and broader society to predict and mitigate the forthcoming impacts of climate change.

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Supplementary documents online:

Supplementary Table S1. Distribution of studies among continents and research themes.

Supplementary Table S2. Details of studies in which whole communities, comprising or including non-vascular cryptogams, were transplanted.

Supplementary Fig. S1. Distribution of transplant studies in Europe, colored by research theme.

Supplementary Fig. S2. Cumulative count of pollution studies in which physiology, pollutants or both were measured.

Supplementary Fig. S3. Country collaboration network of all authors of non-vascular transplant studies (circle size is proportional to frequency of authors from each country, including repeated authors).