

RESEARCH ARTICLE

Do plant traits influence primary succession patterns for bryophytes and vascular plants? Evidence from a 33-year chronosequence on bare chalk

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Abstract

1. During primary succession, the abundance of different species and their associated plant traits change over time. Understanding how plant traits linked to colonising and competitive abilities change through succession is important for determining whether community assembly can be predicted. Examining this across more than one taxon group can reveal if these patterns are generalisable.
2. Here, we investigated primary succession on bare chalk for a chronosequence spanning 33 years for two different taxa, vascular plants and bryophytes. We examined how abundance changed through succession, and how this related to species' colonising and competitive abilities, using relevant plant traits for each taxa. A zero-inflated beta regression model was used to investigate the effects of traits on both presence/absence and abundance-when-present of vascular plants and bryophytes.
3. Vascular plants with a larger specific leaf area were more likely to occur later in succession. Vascular plants, which were hemicryptophytes, wind dispersing and had a lower canopy height, were more likely to increase in abundance-when-present during succession.
4. Bryophytes with a larger spore diameter were more likely to occur later in succession. Shorter bryophytes with a greater frequency of sporophyte production had a higher abundance early in succession, representing their high colonising abilities. Whereas later in succession larger bryophytes, with a mat or weft life form and low sporophyte frequency were more abundant, indicating a shift towards greater competitive abilities.
5. *Synthesis*. This study has revealed different patterns for vascular plants and bryophytes regarding colonisation and changes in abundance through succession, and the associated traits linked to colonising and competitive abilities. Although some traits were found to influence abundance through succession for vascular plants, these were often contrary to the expected pattern representing the change from colonising to competitive abilities, whereas for bryophytes, there was more evidence for this shift with successional age. This suggests that general theories on succession-linked plant traits should not be relied upon in isolation for the

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prediction of community assembly. Context, particularly successional age in relation to the available species pool is also key.

KEYWORDS

beta regression, colonisers, community assembly, competition, perennial stayers, species abundance, species composition

1 | INTRODUCTION

Ecological succession, the process in which biological communities change over time, is one of the oldest themes in ecology (Chang & Turner, 2019; Cooper, 1923; Egerton, 2015). Successional studies are also essential for modern applications, including our understanding of biodiversity loss and threats (e.g. climate change and invasive species), and the need for restoration (Chang & Turner, 2019; Prach & Walker, 2011). The majority of succession studies focus on one taxon group, frequently vascular plants (Coradini et al., 2022; Prach & Walker, 2019). However, examining additional taxa within the same study system is important for understanding whether patterns of change and traits of species present can be generalised and used to predict community assembly.

In succession, it is rare to be able to predict the abundance of individual species at a given point in time; however, it may be possible at the level of the functional group. Plant traits represent important aspects of species' morphologies and life histories, and can be useful indicators for understanding succession. In plants, succession often begins with colonisation from ruderals, which typically have high colonising abilities but low competitive abilities, where competitive ability is defined as the ability of one species to exclude another (Hart et al., 2018). As succession progresses, the environmental conditions and resources influencing the development and survival of plants change, and ruderals are replaced by competitors. Several plant traits have been examined in this context, reflecting the continuum from colonising abilities to resource acquisition strategies (Kahmen & Poschold, 2004; Kelemen et al., 2017; Schleicher et al., 2011). For instance, early colonisers tend to be characterised by smaller specific leaf areas (SLA) and canopy heights, whilst species later in succession tend to be taller and have a larger SLA, reflecting their stronger competitive abilities (Dahlgren et al., 2006; Douma et al., 2012), though this can sometimes vary in certain conditions (Rolhauser et al., 2019). Therophytes (annual plants) usually dominate early in succession, followed by hemicryptophytes (typically herbaceous perennials), whilst phanerophytes (typically shrubs and trees) increase in dominance later in succession (Dölle et al., 2008). Many traits show a trade-off between colonisation and competition; for example seed mass, where smaller seeds are more easily dispersed, but have a lower resistance to environmental hazards (Moles & Westoby, 2004). Furthermore, these patterns may also be influenced by environmental filtering or non-competitive processes, such as climate and soil nutrients (Lasky et al., 2014; Le Bagousse-Pinguet et al., 2017; Li et al., 2022).

Bryophytes are a highly successful group that are able to grow under resource-poor conditions, including relatively impermeable substrates such as rock (Bates, 1998). Despite this, bryophytes have received far less attention with respect to succession compared with vascular plants. The succession of bryophytes is often associated with the life strategy classification developed by During (1979), where 'fugitives' and colonists arrive early during succession, whilst perennial 'shuttle' species and perennial 'stayers' tend to dominate later in succession. As with vascular plants, plant traits can provide useful insights into the abilities of species within these life strategies and the associated succession stage; however, relevant trait data are not always available for bryophytes (Cruz de Carvalho et al., 2019; During, 1979). Life form is an important plant trait for succession and has been utilised in several studies (Cruz de Carvalho et al., 2019; Ezer et al., 2019; Strazdiņa et al., 2013). Although there are several classification systems available for bryophytes (Bates, 1998; Magdefrau, 1982), During (1979) suggested that the bryophyte life forms of dendroids, cushions and wefts are restricted to 'perennial stayers', therefore arising later in succession, whilst short turfs are usually found amongst 'short-lived shuttle species'. Sexual reproduction is another important factor for the establishment and survival of species. Many of the reproductive traits are interrelated, for example, frequency of sporophyte production is often associated with breeding system, since monoicous species produce more sporophytes than dioicous species (Söderström & During, 2005). As with vascular plants, there is often a trade-off between the abilities of early colonisers versus perennial stayers. For instance, the size of the diaspore influences the ability to disperse and establish (Löbel & Rydin, 2010); smaller spores are easily dispersed over longer distances by the wind but larger spores usually establish more readily. Species with small spores tend to produce more spores, but larger spores tend to survive for longer in the diaspore bank (Jonsson, 1993).

Examining how the relationship between plant traits and abundance of species changes during succession can enhance our understanding of these trade-offs, and help us to determine whether differences in abundance are associated with differences in the colonising and competitive abilities of species within the community. Exploring this across more than one taxon can reveal whether the shift from colonisers to competitors, and the associated traits of the dominating species, are consistent across different taxonomic groups during succession. In this study, we examine primary succession on bare chalk within a chronosequence (i.e., a series of

sites with similar attributes that primarily differ in age) spanning 33 years for two different taxon groups, vascular plants and bryophytes. We define this as primary succession, since human disturbance has provided a substrate of exposed bedrock (Walker & Der Moral, 2003). The aims of this study are twofold: first, to assess how the communities of vascular plants and bryophytes change through succession. Second, to examine how the abundance of species change through succession and how this relates to their colonising and competitive abilities. To represent colonising and competitive abilities, we use five species traits for vascular plant species: seed mass, canopy height, SLA, life form and dispersal type; and five for bryophytes: length, perennation, life form, frequency of sporophytes and maximum spore diameter. We make the following predictions:

- (i) Communities of vascular plants and bryophytes will shift through succession, with communities becoming more similar through time. Species richness of vascular plants and bryophytes will increase during early succession, until an intermediate period, after which the number of species will decline.
- (ii) The abundance of vascular plant species with a lower seed mass, canopy height, and SLA will be greater during early succession where colonists dominate, whilst those with a higher seed mass, canopy height and SLA, reflecting a greater competitive ability, will dominate later in succession. Hemicryptophytes will increase in abundance through succession, whilst phanerophytes will appear later. Species dispersed by wind will have a greater abundance earlier in succession.
- (iii) The abundance of bryophytes that are shorter in length, have frequent sporophytes and smaller spores will be greater during early succession where colonists dominate. The abundance of annuals and turf species will also be higher during this time. Later in succession the abundance of longer species, with fewer sporophytes and larger spores will be greater in abundance. Species that are perennial with a cushion or weft life form will also be greater in abundance later in succession.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was undertaken at Down Farm, north Dorset (50°55'51" N, 002°00'15" W), which is located in a rich archaeological landscape (Figure 1). Archaeological investigations were first carried out by Dr Martin Green in 1986, where a 125 m² area was excavated using a mechanical digger (Green, 2000) (Figure S1). Further excavations took place between 2004 and 2018 in May/June, creating a mosaic of bare chalk surfaces, with each plot measuring roughly 400 m². The bulk of the topsoil which was around 30 cm deep, was removed using a mechanical digger followed by hand cleaning with shovels and brooms to achieve a clean bare chalk surface. Soil was dumped around the periphery of the associated excavated plot (Figure S1). The excavations were not backfilled and have remained open and unmanaged (no chemical input or biomass removal has taken place) (Figure 1; Figure S2). The fields surrounding the excavations have fertile chalk soils, 20–30 cm deep and are classified as mesotrophic grassland, British National Vegetation Classification (NVC) (Rodwell, 1992) community MG1 (*Arrhenatherum elatius* grassland). There are also fragments of calcicolous grassland, NVC CG2 (*Festuca-Avenula* grassland) and CG3 (*Bromopsis erecta* grassland) in close proximity.

2.2 | Survey method

A total of 13 transects was set up in July 2019, with one in each of the excavated plots dated 1986, 2004–2008, and 2013–2018 (2 plots were excavated in 2016); each transect measured 16 m (Figure 1). The percentage cover of each vascular plant species was assessed independently in 50 cm × 50 cm quadrats every 1 m along each of the 13 transects, giving a total of 208 quadrats. Vascular plants were identified to species level, with the exception of *Taraxacum* microspecies. Bryophytes were recorded in February 2020 using the same methodology, but with a 20 cm × 20 cm quadrat (Preston et al., 2009).



FIGURE 1 Transects recorded within each of the 13 excavated plots (where year is the plot age at the time of the 2019 survey) (a) at Down Farm, Dorset (b) located in southern England (c). Photos are shown in Figures S1 and S2.

Two plots were not recorded for bryophytes, giving a total of 176 quadrats. The first of which (excavated in 2006) was excluded due to rubble left on the plot, which would have influenced the colonisation of bryophytes and the second plot (excavated in 2016) was excluded due to time constraints, as there was already another plot recorded of this age. Bryophytes were identified to species level (using light microscopy for confirmation where required), with the exception of a few small and/or infertile individuals, where it was only possible to classify specimens to a group level (affecting some *Didymodon* and *Bryum* species).

2.3 | Species traits

Traits representing colonising and competitive abilities were chosen using a literature review. The terms (1) 'primary succession' AND 'plant traits' and (2) 'primary succession' AND 'bryophyte traits' were used as search terms in the Web of Science. The search with plants produced 239 results, whilst only five were identified for bryophytes. Plant traits were selected using the most frequent traits arising from the first 50 relevant results (Table S1): canopy height, dispersal type, life form, SLA and seed mass. SLA, dispersal type, canopy height and seed mass were extracted from the LEDA database (Kleyer et al., 2008), whilst life form was extracted from Grime et al. (2007) (see Table 1 for summary). The bryophyte searches did not yield useful information, although several of the returned papers used Ellenberg indicator values (e.g., Rajandu et al., 2021; Rola et al., 2021); however, these are considered to be ecological preferences rather than plant traits and we did not consider these further (Violle et al., 2007). Instead, we selected traits based on similar studies investigating succession found using alternate search terms in Google Scholar (Fernández-Martínez et al., 2019; Laine et al., 2018;

TABLE 1 Summary of traits analysed for vascular plants and bryophytes.

Name	Type	Units
Vascular plants		
Canopy height	Continuous	m
Dispersal type	Categorical	Wind, animal or unspecialised
Life form	Categorical	Hemcryptophyte, therophyte or phanerophyte
Specific leaf area	Continuous	mm ² /mg
Seed mass	Continuous	mg
Bryophytes		
Length	Continuous	mm
Perennation	Categorical	Annual, annual/perennial or perennial
Life form	Categorical	Turf, mat, weft or cushion/tuft
Sporophyte frequency	Categorical	Occasional/rare or frequent/abundant
Maximum spore diameter	Continuous	µm

Monteiro et al., 2020). The selected traits, length, perennation, life form, sporophyte frequency and maximum spore diameter, were extracted from BRYOATT (Hill et al., 2007). Although some traits can vary widely, such as length, they are still a good indication of size (Hill et al., 2007). For the few individual plants only identified to the genus level (within *Didymodon* and *Bryum*), average traits were calculated using the species recorded within the respective groups, or the most dominant type for the categorical variables (Table 1).

2.4 | Data analysis

Species richness change through succession for vascular plants and bryophytes was investigated using generalised additive models (GAMs), since these are often employed to detect nonlinear patterns (Polansky & Robbins, 2013; Simpson, 2018). Species richness was modelled using a Poisson distribution, with age of plot included as a smoother term, using residual marginal likelihood smoothness selection in the mgcv package (Wood, 2017) in R v4.1.2 (R Core Team, 2022). Model checks and predictor functions were visualised using the gratia package (Simpson, 2021). Non-metric Multidimensional Scaling (NMDS) was used to visualise how the communities varied through succession. Differences in species composition were analysed using the *manylm* function within the mvabund package (Wang et al., 2012), which uses generalised linear models to investigate the potential effect of plot age on the multivariate community. The residual versus fit plots suggested that the data fitted a negative binomial distribution.

To examine the relationships between our sets of colonising and competitive traits on species abundance, we modelled abundance (as proportional plot cover) for vascular plants (range: 0–0.8) and bryophytes (range: 0–0.8) using multilevel beta regression models (Brooks et al., 2017; Miller et al., 2019; Pollock et al., 2012). Beta regression is increasingly being used for proportion data, as it allows typically skewed plant cover data to be modelled without using statistical methods that rely on the normal distribution for quantifying uncertainty (Damgaard & Irvine, 2019; Geissinger et al., 2022). As the beta distribution is restricted to data bounded by 0 or 1 but cannot accommodate these exact values, we used a zero-inflated beta regression model (Damgaard & Irvine, 2019; Keim et al., 2017). This type of regression model involves two processes; the first distinguishes between zeros and non-zeros (i.e., a model of species' presence) and the second uses the beta distribution to model proportional cover (Douma & Weedon, 2019). The effect of each plant trait was modelled separately for vascular plants and bryophytes. We included an interaction between traits and plot age as a fixed effect, to represent our expectation that the effects of traits will change depending on the stage of succession. Although bryophytes were recorded after vascular plants (February 2020 vs. July 2019), we use the same plot age covariates in both models.

Variation across species was included in the model as a random intercept, allowing for the fact that different species in our plots exist with different typical abundances independently of the other covariate effects, and providing shrinkage where species' estimates

are less certain (Gelman & Hill, 2006). Quadrat nested in plot age was also included as a random intercept, however this explained very little of the variance or led to model convergence problems, and was therefore not included in the final models. Continuous variables were centred and standardised by one standard deviation to improve the interpretability of regression coefficients (Schielzeth, 2010). The probability of observing a zero can be modelled as equal for all observations (i.e., without the inclusion of covariates) or this can be modelled using predictors to understand the drivers of vascular plant and bryophyte presence/absence (Douma & Weedon, 2019). We investigate both models, with and without covariates, using an interaction of age x trait and species as a random effect for our predictors. We select the best fitting model based on Akaike Information Criterion (AIC) and inspection of the residuals, although all fitted models are presented in supplementary material. Technically, AIC is an in-sample estimate of out-of-sample predictive accuracy, and has no direct bearing on the causal accuracy of our models; we assume therefore that the best predictive model, as judged by AIC, provides the best description of our system, but strong causal inferences about covariates would require further research (e.g., Arif & MacNeil, 2022).

There could be several weather variables which influence the abundance and/or occupancy of vascular plant and bryophyte species in a given year, for example drought or rainfall (Gao et al., 2018; Jones et al., 2016). However, rather than use modelled climatic outputs as covariates in our model, which themselves have uncertainty, we reside the potential effects of year-to-year variability in the error term within our model. In this study, the omission of weather effects would only become problematic for trait and abundance/occupancy patterns if the annual weather effect influenced the entire time series, which is unlikely.

Since our chronosequence was not fully randomised, we used principal coordinate analysis of neighbour matrices analysis to generate spatial eigenvectors to use as additional predictors to account for the spatial structure of the experiment (Dray et al., 2006). First, a pair-wise geographic Euclidean distance matrix was generated. This was used to create a truncated connectivity matrix, using the minimum spanning tree algorithm to determine the threshold distance. The connectivity matrix was then run through the Moran eigenvector filtering function *ME* in *spdep* (Bivand, 2022; Bivand & Wong, 2018) to identify the most important eigenvectors that reduce spatial dependence, based on a permutation bootstrap test on Moran's *I* for the residuals (Fletcher & Fortin, 2018). The final model, including the spatial eigenvectors ('fitted(ME)'), is therefore:

$$\text{Abundance} \sim \text{Age} + \text{Trait} + \text{Age:Trait} + \text{fitted(ME)} + (1 | \text{Species}).$$

3 | RESULTS

3.1 | Community change in vascular plants and bryophytes

A total of 48 vascular plant species were recorded across the 13 plots (Table S2), with total cover increasing with plot age (Figure S3). The average number of species per plot varied from

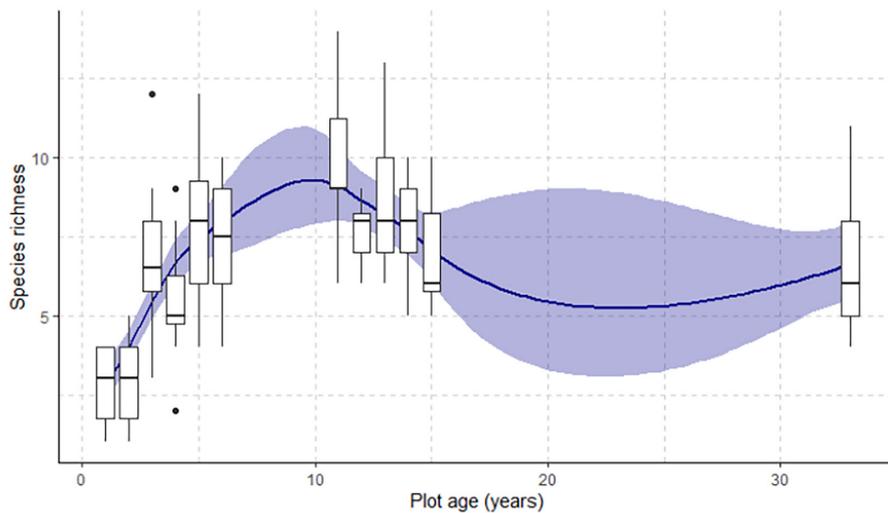
2.8 ± 0.3 (mean \pm SE) for quadrats within the 1-year-old plot, to 9.7 ± 0.6 , the highest number recorded in a plot (11 years old) (for the total number per plot see Table S3). The species richness in plots older than this declined and then levelled off after 14 years (Figure 2a). This is supported by the GAM (Figure 2a), where age as a smoother term provided strong evidence that the pattern between species richness and age of plot was nonlinear ($p < 0.001$, $F = 95.2$, estimated degrees of freedom [edf] = 5.04). Vascular plant communities differed with age of plot (likelihood ratio test [LRT] = 589.5, $p = 0.001$) and appeared to shift along the NMDS 1 axis (Figure 3a). Quadrats within the older plots were positioned closer together, where the axis scores on NMDS 1 were lower. Quadrats within plots with an early or intermediate age were less clustered, suggesting that communities were more similar later in succession. *Leontodon hispidus* and *Dactylis glomerata* were the most abundant species where the axis score on NMDS 1 were low associated with the older plots.

A total of 37 bryophytes were recorded across 11 plots (Table S2), with total cover greatest in quadrats recorded in the 33-year-old plot, followed by the 1-year-old plot (Figure S3). The species richness was highest in the plot aged 14 (6.3 ± 0.4), followed by the 1-year-old plot (5.6 ± 0.3) (Figure 3a). In between these two time points, the lowest species richness is recorded at age six (1.8 ± 0.1). There was strong evidence for this nonlinear pattern, as evidenced by the age smoother term ($p < 0.001$, $F = 76.9$, edf = 4.8). There is greater uncertainty after the age of 15, as there is only one plot older than this (Figure 3d). Bryophyte communities also varied with age of plot (LRT = 613.2, $p = 0.001$), where quadrats within plots aged 1 and 33 were located at opposite directions of NMDS axis 1 (Figure 3b). Quadrats from the 1-year-old plot were associated the colonist *Funaria hygrometrica* and were located towards high values on NMDS axis 1, whilst quadrats from the 33-year old plot were found towards low values of NMDS axis 1 and were associated with the weft species *Calliergonella cuspidata* and *Oxyrrhynchium hians* and *Brachythecium glareosum* both perennial mat species.

3.2 | Colonising and competitive abilities of vascular plants and bryophytes

The multilevel models revealed various relationships between species abundance, their traits and plot successional age for vascular plants (Figure 4) and bryophytes (Figure 5). The models which allowed precision to vary with age and trait were found to have lower AIC values compared to those where precision was fixed for both vascular plants and bryophytes (Table S4) and are shown in Tables 2 and 3, respectively. Results from models with fixed precision can be found in Table S5. The inclusion of the spatial eigenvectors had little impact on the effect size for the fixed factors (except for perennation for bryophytes), so here the models excluding the eigenvectors are presented (see Table S6 for model results with eigenvectors). *p*-values are interpreted on a continuous scale, as a measure of compatibility with the null hypothesis, rather than in a

(a) Vascular plants



(b) Bryophytes

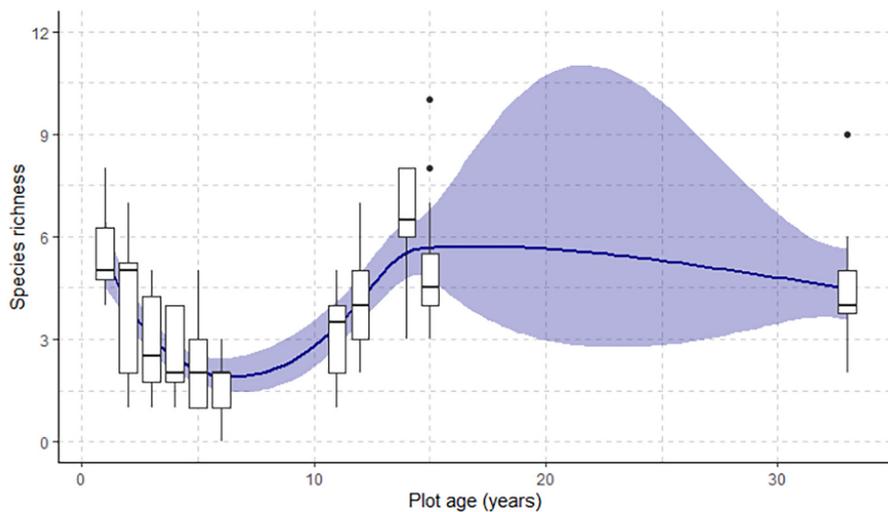


FIGURE 2 Boxplot showing the richness of vascular plants (a) and bryophytes (b) for quadrats recorded within plots aged between 1 and 33 at Down Farm, Dorset. Trend lines in blue represent generalised additive model predictions with 95% uncertainty intervals.

pseudo-Neyman-Pearson, decision-theoretic fashion, as is often erroneously done (Hurlbert et al., 2019; Rafi & Greenland, 2020).

The zero-inflated beta regression models estimated the effect on both presence/absence (see Zi estimates in tables) and the abundance of vascular plants when present (Table 2). The effects of SLA and seed mass on abundance were similar, with no effect of either, the patterns merely reflecting an increase in cover across all species with age. There was, however, strong evidence that the probability of vascular plants occurring increased with plot age and SLA, as indicated by the low p -value for the relevant Zi components in Table 2. Wind-dispersed plants increased in abundance throughout the successional sequence, but this was more pronounced after 15 years, which is likely to be driving the stronger evidence indicated for this effect ($p < 0.001$). Plants dispersed by animals and those with unspecialised mechanisms were largely constant in their abundances. Hemicryptophytes also increased in abundance with plot age particularly after 15 years, whereas phanerophytes and therophytes varied little through succession. There was strong evidence for an effect of canopy height with plot age, whereby shorter plants increased in abundance throughout succession, while taller plants showed little change.

There was strong evidence that bryophytes larger in length, with occasional/rare sporophytes and a mat or weft life form were more likely to increase in abundance-when-present with successional age (Table 3). Although perennials appeared to increase with plot age, while annuals and annuals/perennials tended to decrease, there was very little evidence to support this effect ($p = 0.94$). Bryophytes with larger spores were less abundant at the start but appeared to increase rapidly after the age of 15. However, the already very weak evidence for the effect of spore diameter and age ($p = 0.22$) on abundance, was eliminated with the inclusion of the nested random intercept for quadrat and age ($p = 0.99$). Despite this, there was some evidence for an effect on bryophyte presence/absence, which was stronger with the interaction of plot age, suggesting bryophytes with a larger spore diameter were more likely to occur in older plots.

4 | DISCUSSION

Our understanding of succession is critical for informing community responses to threats such as climate change and habitat

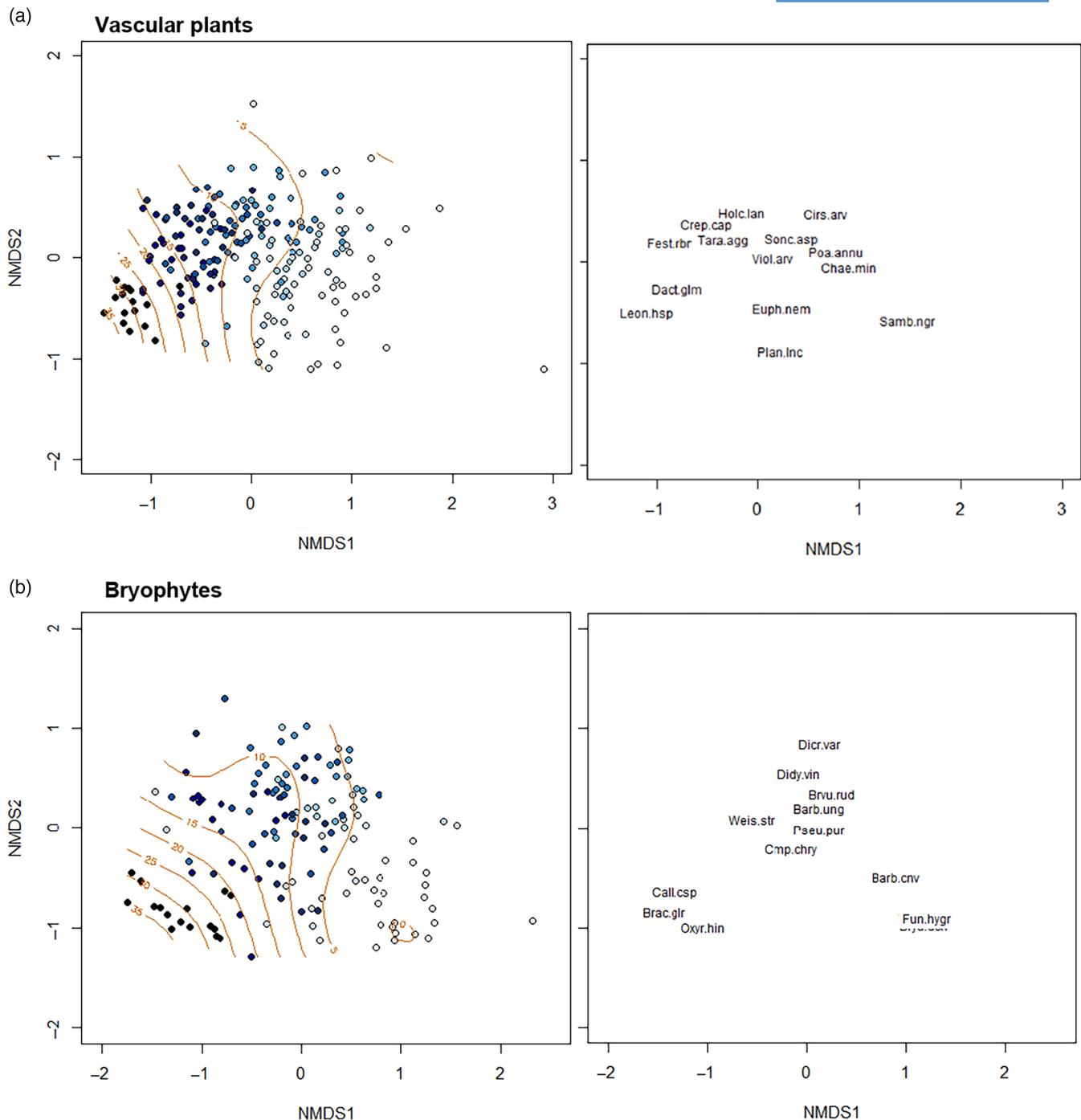


FIGURE 3 Non-metric Multidimensional Scaling (NMDS) plot based on (a) plant species cover (%) from 208 quadrats across 13 plots and (b) bryophyte species cover (%) from 174 quadrats across 11 plots, surveyed at Down farm in plots aged between 1 and 33. Plots are coloured on a gradual scale based on the age of the plot, where light blues are the youngest (1 year) to black, the oldest plot (33 years). Only the most abundant species are labelled (see Table S2 for full species names), in order of relative diversity (using the inverse Simpson index). Contours created using the *ordisurf* function in the *vegan* R package (Oksanen et al., 2007), represent the ages of the plots in years.

fragmentation, but also the potential for restoration. Despite this, our knowledge for some taxon groups such as bryophytes is still limited. Plant traits are an important mechanism to understand patterns through succession, yet few studies have sought broad generalisations in trait-succession dynamics across more than one taxon in the same study system. This study utilises a unique chronosequence spanning 33 years to investigate primary succession on bare chalk for

vascular plants and bryophytes. The use of chronosequences and associated space-for-time substitutions for studying plant succession have been criticised (Damgaard, 2019; Johnson & Miyanishi, 2008), however they are often a necessary tool if change over long time periods is to be evaluated. According to Walker et al. (2010), there are conditions where chronosequences are more appropriate including, (i) studies which evaluate change within short time scales

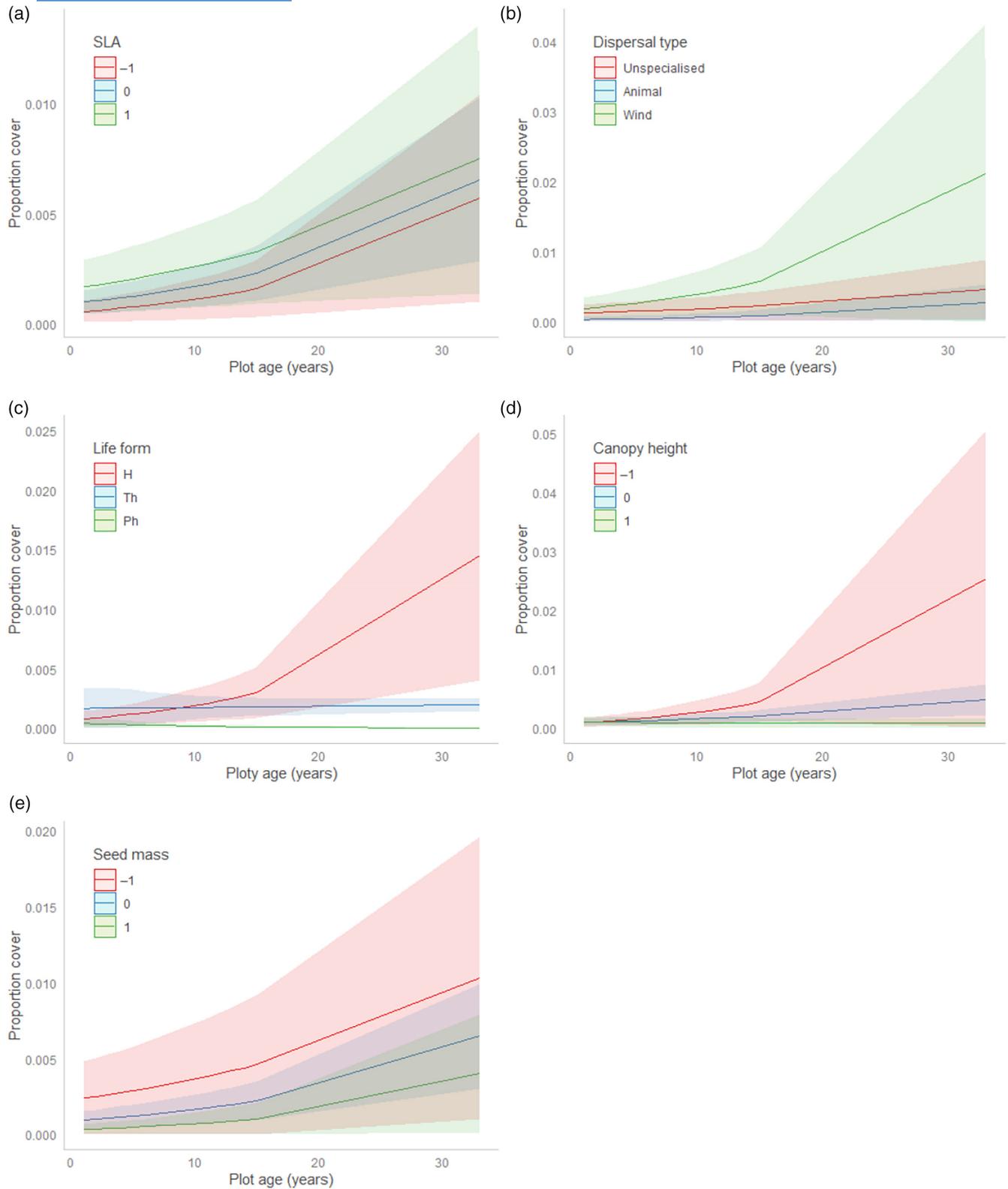


FIGURE 4 Relationship between vascular plant species abundance (measured as proportion cover) and traits; (a) specific leaf area (SLA), (b) dispersal type, (c) life form, (d) canopy height and (e) seed mass, with successional age. Predicted values and confidence intervals (shaded areas) are conditioned on fixed effects and the zero-inflation component. For continuous variables the effects are estimated for the mean, as well as one standard deviation below (labelled -1) and above (labelled 1) the mean (labelled 0).

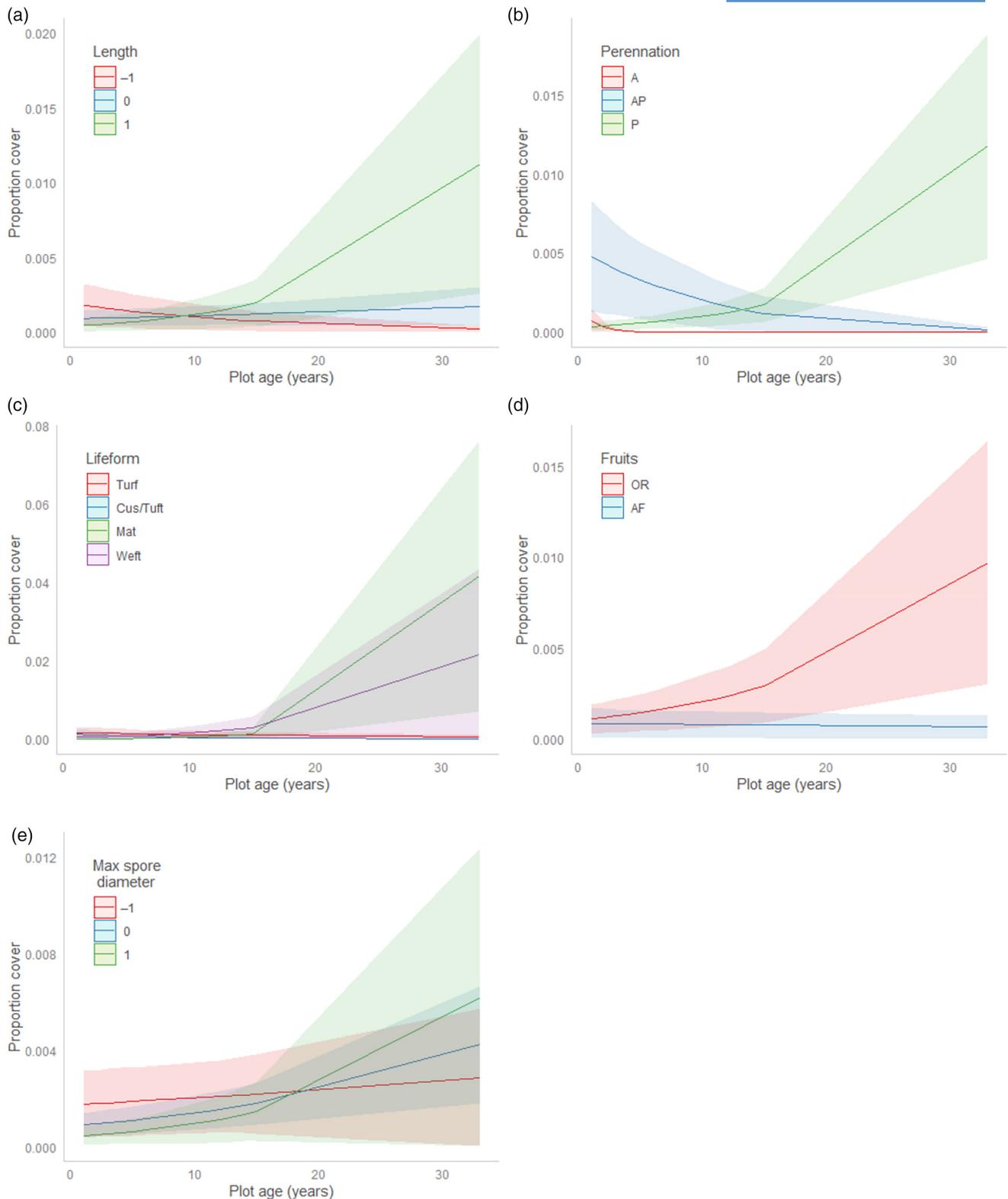


FIGURE 5 Relationship between bryophyte species abundance (measured as proportion cover) and traits; (a) length, (b) perennation, (c) life form, (d) sporophyte frequency (Fruits) and (e) maximum spore diameter, with successional age. Predicted values and confidence intervals (shaded areas) are conditioned on fixed effects and the zero-inflation component. For continuous variables the effects are determined for the mean, as well as one standard deviation below (labelled -1) and above (labelled 1) the mean (labelled 0).

TABLE 2 Parameter estimates (logit scale) of the mixed effect zero-inflated beta regression on the proportion of vascular plant cover according to age and trait (specific leaf area [SLA], dispersal type, life form, canopy height and seed mass). The zero-inflation estimates (logit scale) are denoted with Zi.

Model	Variable	Coefficient	SE	z Value	p-Value
SLA	(Intercept)	-3.58	0.08	-46.13	<0.001
	Age	0.33	0.02	14.96	<0.001
	SLA	0.02	0.08	0.24	0.813
	Age:SLA	-0.00	0.03	-0.09	0.931
	Zi (Intercept)	2.73	0.26	10.67	<0.001
	Zi Age	-0.18	0.03	-5.61	<0.001
	Zi SLA	-0.44	0.26	-1.70	0.090
	Zi Age:SLA	0.11	0.04	2.94	0.003
Dispersal type	(Intercept)	-3.59	0.12	-31.10	<0.001
	Age	0.09	0.04	2.35	0.019
	Dispersal typeAnimal	-0.10	0.16	-0.62	0.536
	Dispersal typeWind	0.05	0.15	0.31	0.759
	Age:Dispersal typeAnimal	0.08	0.05	1.43	0.154
	Age:Dispersal typeWind	0.61	0.05	12.54	<0.001
	Zi (Intercept)	2.58	0.44	5.78	<0.001
	Zi Age	-0.26	0.05	-4.72	<0.001
	Zi Dispersal typeAnimal	0.99	0.59	1.68	0.093
	Zi Dispersal typeWind	-0.74	0.61	-1.20	0.229
	Zi Age:Dispersal typeAnimal	-0.11	0.08	-1.32	0.187
	Zi Age:Dispersal typeWind	0.30	0.07	3.97	<0.001
Life form	(Intercept)	-3.57	0.10	-34.87	<0.001
	Age	0.45	0.03	18.02	<0.001
	Life formPh	-0.26	0.39	-0.66	0.511
	Life formTh	-0.05	0.14	-0.33	0.740
	Age:Life formPh	-0.47	0.22	-2.15	0.032
	Age:Life formTh	-0.35	0.05	-7.51	<0.001
	Zi (Intercept)	2.64	0.36	7.28	<0.001
	Zi Age	-0.34	0.04	-8.09	<0.001
	Zi Life formPh	1.95	1.16	1.69	0.092
	Zi Life formTh	-0.02	0.53	-0.03	0.974
	Zi Age:Life formPh	1.07	0.38	2.75	0.006
	Zi Age:Life formTh	0.40	0.07	5.91	<0.001
Canopy height	(Intercept)	-3.64	0.08	-46.84	<0.001
	Age	0.28	0.03	10.48	<0.001
	canopy_height	-0.21	0.10	-2.18	0.029
	Age:canopy_height	-0.34	0.08	-4.34	<0.001
	Zi (Intercept)	2.73	0.26	10.51	<0.001
	Zi Age	-0.14	0.03	-4.20	<0.001
	Zi Canopy height	0.28	0.26	1.06	0.290
	Zi Age:Canopy height	0.14	0.06	2.26	0.024
Seed mass	(Intercept)	-3.58	0.13	-27.09	<0.001
	Age	0.32	0.05	6.97	<0.001
	Seed mass	-0.06	0.59	-0.10	0.918
	Age:Seed mass	-0.07	0.21	-0.31	0.755
	Zi (Intercept)	2.77	0.26	10.85	<0.001
	Zi Age	-0.20	0.04	-5.10	<0.001
	Zi Seed mass	0.81	0.40	2.05	0.040
	Zi Age:Seed mass	-0.19	0.12	-1.56	0.119

(ca. 1–100 years), (ii) have low biodiversity and (iii) are infrequently disturbed, as with our study. This chronosequence has provided a unique opportunity to investigate the colonising and competitive abilities of vascular plants and bryophytes through succession using plant traits. By examining vascular plants and bryophytes, we determined if these shifts in succession and associated abilities of species present were consistent between different taxa.

4.1 | Community change through succession

We find a nonlinear pattern for the richness of vascular plants between plots aged 1 and 33, supporting our first prediction whereby plants increase during early succession, until an intermediate period, after which the number of species decline. The peak richness was found for plots excavated 11 years before our investigation, and this is likely to reflect the gain in competitive species whilst early colonisers are still hanging on. In plots aged 15 and over, the richness appears to stabilise, with the community becoming more similar. Similar patterns were reported in Anderson (2007), where species richness increased rapidly during early succession until a plateau where gains and losses converged, followed by a subsequent decrease. The richness of bryophytes also showed a non-linear change over time; however, this pattern differed to the vascular plants. Instead, richness was high within the 1-year-old plot and then declined until the 6-year mark. The peak richness occurred slightly later than for vascular plants (14 years) but followed the same trend for plots after this age. This contrasts with other studies in the literature that have identified a continuous increase in the number of bryophytes with succession, however these are often involving epiphytes colonising phanerophytes (De las Heras et al., 1994; Hodge et al., 2009; Turetsky et al., 2010). Hylander et al. (2021) found that the richness of bryophytes increased rapidly from 3 to 42 following fire in Afroalpine heathlands in Ethiopia. However, as with our study they also found that the richness levelled off after 15 years. Hutsemekers et al. (2008) reported a similar increase in the number of bryophyte species over time for slag heaps in Belgium. They suggested that the increasingly dense bryophyte layer provided more appropriate growth conditions for new colonisers. Our conflicting finding of high bryophyte richness in the youngest plot could be explained by germination from the diaspore bank (or temporal dispersal), rather than through dispersal in space. Species in the diaspore bank have the advantage of being present immediately following disturbance and can rapidly colonise early in succession (Jonsson, 1993). The role of the diaspore bank has been studied across a range of habitats (Callaghan et al., 2020; Caners et al., 2009), including chalk grassland. For instance, During and ter Horst (1983) found that 37 species of bryophytes established from soil samples collected in Dutch chalk grassland. The variation in species composition with successional age demonstrated in this study is supported by similar studies which also identified a gradient with age over similar timescales (Esposito et al., 1999; Takashima-Oliveira et al., 2020). Consistent with our findings, Hylander et al. (2021) also found that *Funaria hygrometrica*

was strongly associated with early successional sites. This cosmopolitan species is known to colonise newly disturbed sites around the world, particularly following fires.

4.2 | Plant traits

The use of zero-inflated beta regression models has enabled the effect of different traits to be estimated for both presence/absence and abundance-when-present for vascular plants and bryophytes. We expected that species possessing trait values favourable of colonisation will be more abundant in younger plots representing early succession, whilst those possessing trait values relating to higher competitive abilities will be more abundant in older plots as succession progresses. However, the relationships between vascular plant abundance and presence/absence with traits were variable through succession and did not necessarily support the predictions presented. Vascular plant species were more likely to occur in older plots with a larger SLA, however when present there was no evidence for an effect of SLA on abundance over time. Chang and HilleRisLambers (2019) also found little change with SLA over time when examining community assembly on Mount St. Helens. High SLA usually corresponds with high competitive ability (Dahlgren et al., 2006), however the lack of abundance change through time between the different SLA sizes in this study may be due to the availability of light. In this system, there were still areas of exposed bare chalk to colonise within each plot, and furthermore shade was minimal in this open exposed area, thus competition for light would be less critical. No effect of seed mass was detected for occurrence or abundance of vascular plants with successional age. The expected trade-off would show that good colonisers have lighter seeds and would be more abundant early in succession, while good competitors with heavy seeds would be more abundant later in succession, however our results did not support this. This may be because competition was not highly asymmetric (i.e. the advantage of large seeded species was not strong) in our study (Coomes & Grubb, 2003).

Canopy height, dispersal type and lifeform were all found to influence vascular plant abundance-when-present with age, though the direction of the effect did not necessarily support the predictions presented. For instance, the abundance of species with a lower canopy were more likely to increase with successional age in our plots, particularly in those older than 14 years. Canopy height is often associated with competition for light (Huston & Smith, 1987), hence we would expect species with a higher canopy to be more abundant in older plots. However, one explanation for this in our study system, may be the presence of exposed bare chalk still available to colonise within each plot and consequently because of this competition for light would have been less of a priority compared with colonisation. If the length of the chronosequence were to be expanded beyond this study, then we may see an increase in the abundance of higher canopy species, representing greater competitive ability as more phanerophytes establish and dominate. Similarly, although wind dispersed species

TABLE 3 Parameter estimates (logit scale) of the mixed effect zero-inflated beta regression on the proportion of bryophyte cover according to age and trait (length, perennation, life form, sporophyte frequency (fruit) and maximum spore diameter). The zero-inflation estimates (logit scale) are denoted with Zi.

Model	Variable	Coefficient	SE	z Value	p-Value
Length	(Intercept)	-3.69	0.08	-43.93	<0.001
	Age	0.17	0.05	3.30	0.001
	Length	-0.02	0.05	-0.28	0.777
	Age:Length	0.19	0.04	5.03	<0.001
	Zi (Intercept)	3.04	0.27	11.22	<0.001
	Zi Age	-0.01	0.05	-0.14	<0.892
	Zi Length	-0.06	0.27	-0.23	0.818
	Zi Age:Length	-0.57	0.05	-12.55	<0.001
Perennation	(Intercept)	-3.82	4.79	-0.80	0.425
	Age	0.00	5.28	0.00	1.000
	Perennation_AP	0.11	4.79	0.02	0.981
	Perennation_P	0.10	4.79	0.02	0.984
	Age:Perennation_AP	-0.11	5.28	-0.02	0.984
	Age:Perennation_P	0.43	5.28	0.08	0.935
	Zi (Intercept)	10.55	3.85	2.74	0.006
	Zi Age	7.33	4.15	1.77	0.077
	Zi Perennation_AP	-8.18	3.88	-2.11	0.035
	Zi Perennation_P	-7.39	3.87	-1.91	0.056
	Zi Age:Perennation_AP	-6.46	4.15	-1.56	0.119
	Zi Age:Perennation_P	-7.91	4.15	-1.91	0.056
Life form	(Intercept)	-3.75	0.09	-40.21	<0.001
	Age	0.03	0.07	0.47	0.637
	Life form_Cus/Tuft	0.10	0.20	0.50	0.618
	Life form_Mat	-0.23	0.18	-1.32	0.186
	Life form_Weft	0.02	0.15	0.16	0.877
	Age:Life form_Cus/Tuft	-0.37	0.25	-1.46	0.145
	Age:Life form_Mat	0.62	0.11	5.61	<0.001
	Age:Life form_Weft	0.39	0.11	3.51	<0.001
	Zi (Intercept)	2.86	0.36	7.84	<0.001
	Zi Age	0.38	0.07	5.38	<0.001
	Zi Life form_Cus/Tuft	1.04	0.78	1.34	0.181
	Zi Life form_Mat	0.76	0.77	0.99	0.321
	Zi Life form_Weft	-0.21	0.81	-0.26	0.792
	Zi Age:Life form_Cus/Tuft	0.35	0.25	1.38	0.169
	Zi Age:Life form_Mat	-1.65	0.14	-11.78	<0.001
Zi Age:Life form_Weft	-1.09	0.12	-9.04	<0.001	
Fruit	(Intercept)	-3.54	0.08	-41.80	<0.001
	Age	0.37	0.05	8.09	<0.001
	Fruit_AF	-0.09	0.09	-1.03	0.302
	Age:Fruit_AF	-0.38	0.09	-4.13	<0.001
	Zi (Intercept)	2.56	0.34	7.47	<0.001
	Zi Age	-0.26	0.05	-5.13	<0.001
	Zi Fruit_AF	0.86	0.52	1.66	0.098
	Zi Age:Fruit_AF	0.32	0.10	3.41	<0.001

TABLE 3 (Continued)

Model	Variable	Coefficient	SE	z Value	p-Value
Maximum spore diameter	(Intercept)	-3.55	0.08	-44.62	<0.001
	Age	0.27	0.04	6.08	<0.001
	Max spore diameter	0.11	0.08	1.28	0.200
	Age:Max spore diameter	0.10	0.08	1.23	0.219
	Zi (Intercept)	2.96	0.26	11.42	<0.001
	Zi Age	-0.18	0.04	-4.17	<0.001
	Zi Max spore diameter	0.52	0.28	1.86	0.063
	Zi Age:Max spore diameter	-0.21	0.06	-3.44	<0.001

tend to decrease with succession (Ecke & Rydin, 2000; Karadimou et al., 2018), we found the opposite pattern where wind dispersed species increased in abundance with age, particularly after the age of 15. Prach et al. (1997) also found increases in both wind and animal dispersed species through succession and suggested this was because many of the early colonists do not possess specific modes of dispersal. Hemicryptophytes were the only group to increase in abundance through succession, as predicted, whilst therophytes and phanerophytes remained largely constant. We expected annuals to dominate early in succession since colonisers often have an annual life cycle, whilst tree seedlings would appear later in succession as evident in other succession studies (Ecke & Rydin, 2000; Prach et al., 1997; Rehounková & Prach, 2006). However, the sample size for phanerophytes was very small (*Sambucus nigra*, *Crataegus monogyna* and *Prunus spinosa*) with low numbers recorded across a few plots which ranged in age. In our study system, it is possible that a longer chronosequence would be required before any increase in phanerophytes may be detected.

Several relationships between bryophyte abundance and traits were detected with successional age, many of which supported our predictions representing the shift from colonists to perennial stayers. The shift was often apparent around 14 and 15 years, where changes in abundance for particular trait attributes were detected. For example, the abundance of shorter bryophytes declined slightly with age, whilst longer species increased in abundance, as predicted, particularly in plots older than 15 years. Length, indicating size, is an important competitive trait since larger bryophytes can overshadow smaller bryophytes, and/or monopolise a larger area of space or resource (Söderström & Gunnarsson, 2003); thus, we interpreted this increase in longer species in older plots as the shift during succession to perennial stayers. The bryophyte length is likely to be associated with the increase in the abundance of perennial bryophytes, which also appear to increase more rapidly in plots older than 14 years, however there was no evidence for this effect and very weak evidence for an effect on presence/absence. This effect may become more apparent with a longer chronosequence, as Hutsemekers et al. (2008) report an accumulation of perennial stayers with slag heaps that have been colonised for 50 years. Only three annuals were recorded in very low numbers (*Ephemerum recurvifolium*, *Microbryum davallianum* and *Microbryum rectum*), so the relationship could not be assessed reliably; however, all three species

were found in 1- or 2-year-old plots, which supports the idea that colonisers early in succession often have an annual life cycle.

The reproductive traits varied in their support for the shift from colonists to competitor during succession in this study. Species with a low sporophyte frequency were more abundant later in succession, reflecting their ability to compete for resources. However, there was little evidence of an effect of spore diameter on abundance, though bryophytes were unlikely to occur in younger plots with a small spore diameter. Laine et al. (2018) found the converse when examining mire development in Finland; spore size increased during succession, but no pattern was found for the frequency of sporophytes. Bryophytes with a mat or weft life form increased in abundance during succession, whilst cushions/tufts decreased and turfs remained constant throughout the aged plots, thus only partially agreeing with our predictions. During (1979) suggests that perennial stayers which are more frequent in later successional stages tend to be wefts, dendroids, mats and large cushions. This supports our findings for mat, weft, and turf species, with the latter remaining consistently low with successional age; however, the decline in cushions and tufts was unexpected.

This study reveals different patterns for vascular plants and bryophytes with respect to the abundance of species and plant traits representing the continuum of colonising and competitive abilities through succession. We find for vascular plants, although some traits were found to influence abundance through succession, these were often contrary to the expected pattern representing the change from colonising to competitive abilities. For example, an increase in abundance through succession for wind dispersers with a lower canopy height. However, for bryophytes there was more evidence for this shift with successional age using the plant traits. Shorter species with a greater frequency of sporophytes had a higher abundance early in the succession representing their high colonising abilities. Whereas later in succession bryophytes, with a mat or weft life form and low sporophyte frequency were more abundant, indicating a shift towards greater competitive abilities. Previous studies have demonstrated the shift in colonising and competitive traits through succession. For instance, Zhang et al. (2018) found that plant traits associated with plant colonising and competitive ability influenced species abundance during secondary succession on a subalpine meadow, Qinghai Tibetan Plateau. The abundant species during early succession were found to have high photosynthetic rate, high leaf proline content, low

seed mass and low seed germination, therefore having high colonising abilities. Later in succession species with large seeds, high seed germination, low photosynthetic rate and low leaf proline content were more abundant, representing greater competitive abilities. However, other studies have suggested that plant traits are not associated with successional patterns, even where the traits examined are selected to represent the processes important in succession (Chang & HilleRisLambers, 2019; Schleicher et al., 2011; Silva et al., 2017). Chang and HilleRisLambers (2019) examined primary succession sites in Mount St Helens, Washington USA, following a volcanic eruption and suggested that successional processes are less generalisable than suggested. They suggested that legacy effects and local-scale environmental factors were important for determining community assembly. Our findings partly support the idea that traits for predicting community assembly for succession is less generalisable than often claimed. Environmental filtering may have also contributed to the patterns evident in this study. For instance, Maire et al. (2015) found that globally two leaf traits (stomatal conductance and leaf nitrogen) were influenced by soil pH, soil available P and the climatic moisture index. However, environmental filtering is typically challenging to assess, since the data utilised in many studies is often too broad to test reliably (Kraft et al., 2015). Although bryophyte abundance during succession was associated with some plant traits linking colonising and competing abilities, this shift was less obvious for vascular plants. This suggests that consistent patterns across different taxonomic groups should not be presumed. For example, traits that related to size affected abundance for bryophytes (length), but only occurrence for vascular plants (SLA). The differences between the shift in colonising to competitive abilities for bryophytes and vascular plants may arise because vascular plants are more dependent upon the local species pool and their associated dispersal abilities compared with bryophytes, which are efficient dispersers over long distances (Barbé et al., 2016; Vanderpoorten et al., 2019). The excavated plots were surrounded by arable, improved areas and a hay meadow (see Table S7 for vascular plant species list within each). Vascular plants which were recorded more frequently in the experimental plots, particularly for the older plots, tended to have a greater abundance in the hay meadow including *Leontodon hispidus*, *Festuca rubra* and *Plantago lanceolata*, which illustrates the influence that the surrounding vegetation can have on colonisation. Furthermore, the successional age is also an important factor driving the species available.

4.3 | Implications and conclusions

There has been considerable research on primary succession, with many studies undertaken in such environments as volcanoes (Barba-Escoto et al., 2019; Karadimou et al., 2018), glaciers (Fickert et al., 2017; Franzetti et al., 2020) and sand dunes (Martínez et al., 2001; Nylén & Luoto, 2015). However, fewer studies have investigated this process on bare chalk (Burnham, 1990; Hope-Simpson, 1940; Tansley & Adamson, 1925), particularly for bryophytes (e.g. Preston et al., 2009). This study has therefore provided

insight into primary succession on a less studied substrate for two different taxon groups. Understanding succession on bare chalk is more important than ever, with declines in the quantity and quality of calcareous grassland across Western Europe (Fuller, 1987; Poschod et al., 2005; Ridding et al., 2015) and increasing interest in the potential for restoring this habitat of high conservation value (Kiehl et al., 2010). This has been highlighted using the same study site in Hawes et al. (2020). Our current study has shown the different accumulation patterns of vascular plants and bryophytes through succession, with the richness of both taxa stabilising after 15 years. Although the richness for both taxa at this stage was fairly low, if the goal was to achieve a species-rich calcareous grassland, seeding alongside natural regeneration could enhance the number of species, since restoration success is often limited by the availability of seeds in the surrounding landscape (Scotton, 2018; Smith et al., 2017).

Our study being one of the few to examine trait-succession generalisations using vascular plants and bryophytes, has revealed that it is difficult to predict community assembly at specific time points for different taxa using plant traits alone. We found evidence of an effect for some traits on presence/absence only, whilst others also influenced abundance-when-present through succession, albeit not always in the expected direction. Factors such as successional age and the surrounding environment, which influence the species available, are also key to driving abundance change during succession and should be considered in future research.

AUTHOR CONTRIBUTIONS

Lucy E. Ridding, Peter Hawes, Richard F. Pywell and Oliver L. Pescott conceived the research idea and designed the field methodology; Lucy E. Ridding and Oliver L. Pescott designed the analysis; Lucy E. Ridding, Peter Hawes, Robin Walls, Sharon L. Pilkington and Oliver L. Pescott collected the data; Lucy E. Ridding performed statistical analyses with contributions from Oliver L. Pescott. Richard F. Pywell acquired funding. Lucy E. Ridding led the writing of the manuscript; all authors discussed the results and commented on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

These data are published and freely available via the Environmental Information Data Centre (EIDC) <https://doi.org/10.5285/358eb380-74a0-4acd-9df2-696fdf13a6d7> (Ridding et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Overview of the excavated plots at Down Farm, north Dorset.

Figure S2. Photos of each of the excavated plots aged between 1 and 33 at Down Farm, north Dorset.

Figure S3. Boxplot showing the total cover of vascular plants (A) and bryophytes (B) for quadrats recorded within plots aged between 1 and 33 at Down Farm, Dorset.

Table S1. Plant traits used in two or more studies arising from the first 50 papers returned from the Web of Science using the terms “primary succession” AND “plant traits”.

Table S2. A list of the 48 vascular plants and 37 bryophytes found at Down Farm, Dorset. Those marked with an asterisk are found in Figure 3.

Table S3. The total and average number of vascular plants and bryophytes recorded within plots aged between 1 and 33 at Down Farm, Dorset.

Table S4. Akaike Information Criterion comparison of zero-inflated beta regression on the proportion of plant and bryophyte cover according to age and trait with a fixed and variable precision.

Table S5. Parameter estimates (logit scale) of the mixed effect zero-inflated beta regression on the proportion of vascular plant and bryophyte cover according to age and trait (length, perennation, life form, sporophyte frequency (fruit) and maximum spore diameter) with precision fixed.

Table S6. Parameter estimates (logit) of the mixed effect zero-inflated beta regression on the proportion of vascular plant and bryophyte cover according to age and trait with varying precision and spatial eigenvectors included (maximum of 5 spatial eigenvectors presented—"fitted(abund.ME.xx)").

Table S7. Species lists for vascular plants recorded via a rapid walkover survey on the 18 July 2019 in each of the three areas surrounding the experimental plots; an improved area, arable fields and a hay meadow (P=present).

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