Physically, physiologically and conceptually hidden: improving the description and communication of seed persistence

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Running title: Seed persistence and niche theory

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Abstract

Seed persistence is a trait that is difficult to observe or measure and, consequently has remained conceptually obscure for 40 years since Grubb's influential description of the regeneration niche. Seed persistence is the ability of seeds to persist in a viable state post-dispersal and is relevant to current research in plant community dynamics and conservation. However, categorisations of seed persistence as transient, short-term or long-term persistent do not acknowledge the variation in persistence times as a result of deterministic processes and are difficult to apply in a predictive capacity. Consequently, a more robust understanding of seed persistence is needed in niche descriptions that are temporally explicit and in predicting the distributional changes of species in the current and future climate. We surmise an alternative to the categorizations of seed persistence on the basis of seed bank type and argue that it is best expressed as a continuous variable. We review the methods available for estimating seed persistence in situ and provide a number of testable hypotheses to contribute to the development of this important research topic. We maintain that seed persistence has not been incorporated adequately into niche theory and highlight that it can make several contributions including properly defining metapopulation niche, population growth definition. This holistic approach by integrating seed persistence into niche theory would allow us to better predict the survival of plants in a changing environment.

Key words: climate change; dormancy; ecological niche; soil seed banks; longevity index.

Introduction

Seed persistence is a trait that is extremely difficult to quantify: the physiological processes controlling persistence are contained within the external layers of the seed, the seeds themselves are physically hidden once they are buried beneath the soil surface, and as a consequence, seed persistence has remained conceptually obscure for 40 years since Grubb's (1977) influential description of the regeneration niche. Significant attention has been given to conditions promoting germination and seedling establishment, two important components of this niche, and these are proving to have enduring relevance, most recently with respect to understanding vegetation response to climate change and other drivers of range loss (e.g. Cochrane et al., 2015; Holt, 1990; Walck et al., 2011). However, one aspect of the regeneration niche, the ability of seeds to persist in the soil, continues to be largely overlooked by a significant part of the plant ecology community. Seeds of most plant species persist for varying time periods after dispersal and before they germinate (Chambers and MacMahon, 1994; Roberts, 1981), and as Grubb (1977) noted, this ability is "probably extremely important" for maintaining the rarest species within a community. However, whilst Grubb (1977) made contributions that are now several decades old, and more authors before and since have recognized the ecological relevance of seed persistence (e.g. Gremer and Venable, 2014; Venable and Brown, 1988), existing definitions of seed persistence have failed to resonate with the wider ecological research community meaning that seed persistence is an overlooked and misunderstood property of populations and species. While efforts to determine persistence ability should continue, two recent attempts (Long et al., 2015; Saatkamp et al., 2018) have called for a more rigorous treatment to define seed persistence, implying that more robust approaches are imperative in linking seed persistence with niche theory.

Many detailed studies conducted in various ecosystems have identified numerous seed- and soil-related factors that impact upon seed persistence in soil and previous reviews highlight our lack of understanding of the interactions of these factors (Baskin and Baskin, 2006; Benech-Arnold et al., 2000; Chambers and MacMahon, 1994; Long et al., 2015; Thompson, 2000). Despite growing evidence that multiple factors together drive persistence and germination, and that seed persistence at species- and individual-level is extremely variable (supplementary data provides an overview of factors known to influence the entry and exit of seeds in the soil), seed persistence is categorized as soil seed bank longevity at species-level based on estimates of time from dispersal until germination or death. This review aims to improve on the current systems of seed bank classification by bringing together several areas of research (physiology, community ecology and theoretical ecology) to i) demonstrate that existing seed bank classifications have served a useful purpose, but are now inadequate for current research questions pertaining to the wide range of seed bank research, ii) to reconcile definitions of persistence with ecological niche theory and iii) make recommendations for reporting seed persistence that can be more effectively applied to predicting population survival and species viability.

Current seed bank classifications

The formation of a seed bank commences when seeds reach the soil surface and ends with the germination or death of seeds (Chambers and MacMahon, 1994; Jaganathan et al., 2015). In most cases, seeds are dispersed from a parent plant at the end of the growing season which is followed by harsh climatic conditions e.g. the dry seasons in the Tropics or cold winters in alpine ecosystems (Baskin and Baskin, 2014). To avoid seedling death, the seeds must therefore possess mechanisms to promote persistence at least until the next favourable germination period followed by a growing season (see supplementary data). Germination is typically concentrated in the first post-dispersal growing season, but may continue for many years, albeit in seasonal cycles (Baskin and Baskin, 2014; Thompson, 2000). Thompson and Grime (1979) classified soil seed banks as transient and persistent . Transient seed banks persist in the soil for < 1 year, i.e. at least until the first opportunity for germination occurs, but species forming persistent seed banks maintain viable seeds in the soil for > 1 year. Seed banks are a component of a population that generally persist over consecutive years maintained by a turnover of seeds entering and leaving the soil.

This classification scheme has subsequently been revised by numerous researchers, mostly when studied species failed to fit into the original categories (Csontos and Tamás, 2003; Grime, 1981; Hawkins et al., 2007). Several authors noted that treating all seed banks persisting for >1 year as functionally the same (i.e. classing them all as ‘persistent’), could not convey the huge potential for variation in persistence times (Bekker et al., 1998; Poschlod and Jackel, 1993; Thompson et al., 1997). This led to further distinctions between transient, short-term persistent and long-term persistent (Bakker et al., 1996; Bakker, 1989), although the length of time suggested as defining each of these sub-categories varied from 1-4 or 5 years to a decade (Csontos and Tamás, 2003; Walck et al., 2005).

Despite the successive refinements, existing soil seed bank classifications may be inaccurate because they do not acknowledge that i) different methods produce varying estimates of seed persistence leading to misclassification, and ii) many seed- and soil- related factors contribute in varying magnitudes and sometimes with additive or synergistic impacts on persistence times at different locations (Long et al 2015; supplementary data). These problems mean that community ecology has often overlooked seed persistence. The review of community ecology studies undertaken by Jiménez-Alfaro et al. (2016) supports this observation; of 226 studies only 3.2% included seed longevity as a trait to describe and understand community-level processes. Given that soil seed bank classifications appear to be underutilised and authors circumvent the persistence issue rather than deal with the current systems, we recommend that alternative approaches to describing seed persistence are adopted.

Methods for measuring seed persistence

The ability of seeds to persist in soil is long-established (Darwin, 1859), but only since the 1970's have methods been developed to estimate the duration of persistence. According to Saatkamp et al. (2009) these methods can be classified into: (a) radio-carbon dating of seeds present in soil (McGraw et al., 1991); (b) artificial burial of seeds in soil and retrieval at regular intervals to test germinability or viability (see below); (c) determination of the depth distribution of germinable seeds in the soil (Bekker et al., 1998); (d) determination of soil seed banks along successional series (Poschlod et al., 1998) and (e) comparative analysis of seasonal dynamics of seed rain and seed bank (Thompson and Grime, 1979, Poschlod and Jackel, 1993). We also add to these the use of autogenous recovery of vegetation after anthropogenic vegetation clearance.

Each method has advantages and disadvantages (Thompson et al., 1997, Saatkamp et al., 2009). For example, recent seed input from standing vegetation at unknown distances from the sample can 'contaminate' the data, and germination under controlled conditions incorrectly assume a uniform response thereby interpreting lack of germination as seed death. Radio carbon dating is the most reliable and has well-defined confidence limits but is extremely time-intensive especially given the seed-to-seed variation in persistence, meaning that large samples are necessary to represent variation. Another drawback is the destructive nature of radio-carbon dating meaning that the viability of seeds used for analysis cannot be determined.

Artificial burial is generally regarded as the most accurate and frequently used method of describing in-soil seed persistence (e.g. Schwienbacher et al., 2010) but is not without limitations. Firstly, burial depths are often limited to 5cm (Baskin & Baskin, 2014) because seeds buried in the top soil layer are assumed to experience 'optimal' conditions for both dormancy break and germination, but seeds buried at lower or shallow layers may germinate, die or remain viable for many years (Hu et al., 2009, Campbell and Nicol, 2002). However, this may not necessarily be true for all the species, e.g. for *Avena ludoviciana*, which remained dormant at the soil surface, dormancy was broken in a higher proportion of seeds found at a depth between 5 and 15 cm than seeds buried below 15 cm where the seeds remained dormant (Salimi and Angadji, 1997). Likewise, in a two year artificial burial experiment, Wijayratne & Pyke (2012) showed that seeds of *Artemisia tridentata* Nutt. subsp. *tridentata* and *Artemisia tridentata* subsp. *wyomingensis* buried at 3 cm below the soil surface retained 30-40% viability when exhumed at the end of 2 year period compared to 0 and < 11% of seeds survived on soil surface from each species respectively. Harrison et al. (2007), working with *Ambrosia trifida*, revealed that seeds buried in the top soil layer had no viable seeds at the end of fourth year, whereas 19% of the seeds remained viable at the 20 cm burial depth and some seeds at this depth remained viable even after 9 years. If burial experiments were conducted only at top soil layer, then this species might be classified as short-term persistent, because no viable seeds remained after four years. Consequently, burial experiments conducted at one particular depth are likely to result in misclassifications of seed bank type. Furthermore, it is important to note that seeds can be buried by various routes including wind-deposited soil particles, root growth loosening the soil, rainfall making top soil layers muddy and therefore, fluid, trees uprooting, and landslides (Long et al., 2015), all of which effectively alter the depth of burial even as the trial is underway.

Secondly, seeds of the same species buried at multiple sites show variance in persistence as multiple sites represent more variation in key explanatory variables and therefore viability over time varies with site (Quinlivan, 1967, Robocker et al., 1969). One case described by Robocker et al. (1969) is pertinent to this: during a 10 year burial trial of *Halogeton* seeds comparing two different colours of seeds, those authors found that none of the black seeds buried in Nevada, Utah and Washington persisted after one year in the soil (persistence ended through germination or seed death). However, 67% of the brown seeds retrieved from Washington germinated successfully.

Thirdly, the duration of burial in experiments described in the literature varied from a few months to 11 years which may place an artificial endpoint on persistence estimations [see chapter 7 of

Baskin and Baskin (2014)]. It is often not known if burial experiments were planned for a set time period and if the species investigated had some viable seeds beyond the experimental period. To quote one example, seeds of *Chrysocephalum apiculatum* sown on the surface and buried at 5 cm depth had 36% and 61% viable seeds after 12 months respectively, but the experiments were terminated and it remains unknown if this species can be included in short-term persistent or persistent category (Lunt, 1995).

Besides the traditional estimation methods, several novel techniques show promise in determining the seed persistence in soil. We searched the literature to identify new methods of estimating seed persistence in soil and found 13 techniques that have been frequently used to track seed movement in soil after dispersal, most of which are reviewed in Forget and Wenny (2005). Some of these methods might also be used to estimate seed persistence, e.g. radio tracking for larger seeds (Pons and Pausas, 2007). Given its ease and precision in identifying the exact location of seeds, post-dispersal seeds can be recovered routinely after some time and tested for viability. Dyeing seeds for consecutive years at the natural maturation time with different colors each year before performing soil core analysis annually can also determine persistence times although not all seeds can be recovered. The isotope method proposed by Carlo et al. (2009), involves spraying 15N-urea during seed maturation and identifying the isotopically enriched seedlings, but this technique could only determine the persistence time of germinated seeds and information about seed death cannot be determined. However, it is of interest to note that these methods have been used rarely for persistence estimation and incorporating them in new attempts would go long way.

Attempts to improve the description of seed persistence in the soil

The problems with seed bank classifications have been acknowledged by previous researchers and has resulted in attempts to coalesce the varying seed persistence estimates produced by different methods, e.g. artificial burial, radiocarbon analysis, and removal of soil cores to identify seeds. Thompson et al. (1998) developed a longevity index (LI) from the various persistence classifications (i.e. transient, persistent) reported for a given species. The LI is the proportion of the total number of published seed bank classifications (i.e. the sum of transient, short and long-term persistent records) that are persistent and is expressed as a value between 0 (fully transient, i.e. all the records reported transient seed bank type) and 1 (fully persistent, i.e. all the records reported long-term persistent seed bank type). Although this technique reports seed persistence on a continuous scale and has been widely used, Saatkamp et al. (2009) questioned the approach, as the seed bank types suggested by their burial experiment did not agree with the LI classification. This problem is likely to occur in many situations, as the new data generated for persistence of a particular species would continue to alter the LI and there may be a bias, as species of a certain type of habitat or with a certain type of seed persistence may be overrepresented. Thus, we note that not only is the LI prone to errors based on how the estimates of persistence were generated, it actually obscures important variation in seed traits that could improve the application of seed persistence data to the predictive requirements of current ecological research.

Various theoretical and/or mathematical models have been developed to predict the fate of seeds after dispersal and until germination (Gardarin et al., 2012; Holzapfel et al., 2006). Whilst these models are highly useful, their application to community ecology is still challenging, either due to the limitations imposed by climatic regime, e.g. models developed for arid systems with seasonal temperature extremes cannot be used for rainforests (Lampei et al., 2017), or restricted to specific sets of species, e.g. weeds or annuals (Petrů et al., 2006). Furthermore, most models ignore the fact that seeds can be dispersed to different environments or micro-sites, e.g. they might be deeply buried, where persistence may be favored or seeds might die quickly (Saatkamp et al., 2011; Vázquez-Yanes and Orozco-Segovia, 1982; Venable and Brown, 1993). In their recent comprehensive review, Long et al. (2015) propose a theoretical framework for describing seed persistence on a continuous scale that attempts to encompass all scenarios by identifying a wide range of explanatory variables affecting persistence times. They conceptualize this as a three-dimensional space in which seed persistence is determined by the interacting dimensions of exposure to persistence-limiting variables and traits conferring resistance to seed death or germination. This paper has made a significant contribution to our understanding of seed persistence and certainly provides a more robust approach to predicting seed persistence, but we argue that the resistance-exposure model has some limitations. The first is that it does not explicitly state that seed persistence estimates are specific to one set of conditions and cannot be automatically extrapolated to other situations. Seeds are known to persist longer in certain micro-sites compared to others, but this has not been given any consideration by Long et al. (2015) and other models available. Secondly, Long et al. (2015) suggest that hypothetically, a given trait promoting persistence might offset an environmental parameter that limits seed persistence; consequently, the model might be erroneously interpreted as a simple trade-off between two opposing processes. In reality, persistence-limiting variables rarely work in isolation: the response of seeds to changes in these conditions is rarely linear, and these variables may become irrelevant above or below key thresholds and/or change in severity depending on the levels of exposure to other persistence-limiting conditions. Thirdly, Long et al.'s (2015) model assumes that conditions identified as 'exposure' parameters will always limit persistence thereby reducing seed survival relative to the maximum seed longevity identified under controlled conditions. However, it is possible that persistence may be promoted by certain variables or traits that in other circumstances might also curtail survival e.g. they provide the example of seed coat toughness, which can promote longevity by protecting the internal tissues of the seed, but can also be a barrier to successful germination when soil moisture is too low to allow the seed coat to split and the cotyledons to emerge.

Defining seed persistence as a continuum

In advocating the description of seed persistence as a continuous variable, we support the use of the unit recommended by Long et al (2015) - the time period over which 50% of a population of seeds have persisted since maturation on the parent plant. This type of metric is typical for any process which has the potential to last for time periods which are practically impossible to measure e.g. the decay of radioactive substances is expressed as the ‘radioactive half-life’. This measure has also been used previously, e.g. mortality over time in seeds stored in gene-banks (Pritchard and Dickie, 2003), and whilst representing an arbitrary threshold of 50% survival, avoids the complications presented by the ‘long tail’ of seed persistence estimates resulting from the extremely long persistence of a small proportion of a population. Although this might be perceived as obscuring some of the variation that this review emphasizes as being important, this is the only feasible way of conveying seed persistence times. Where persistence times are reported, they should be linked to the conditions under which the persistence estimate was made in order to determine whether variation in persistence exists and whether this can be linked to particular explanatory variables.

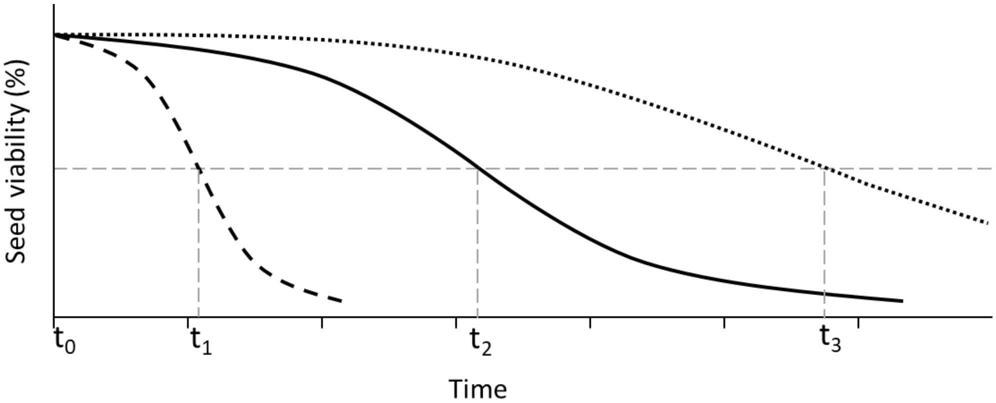

Figure 1. Scenarios of seed viability as a percentage of initial viability of a sample of seeds over time (year) from point of maturation (t_0). Horizontal dashed line refers to 50% mortality or germination; vertical dashed lines denote time at which 50% mortality or germination occurs for three samples of seeds.

Figure 1 demonstrates how the persistence time (time taken since maturation for 50% of the population to die) can be assigned to three samples of seeds. This hypothetical scenario borrows the sigmoidal curve identified in seed decay in storage conditions (Mead and Gray 1999). The three samples might represent different species or populations of the same species, or might represent samples from plants of the same species and population but in different microsites. Mean persistence time to 50% mortality or germination may be expressed with an appropriate measure of variance around the mean. Thus, a proportion of seeds belonging to a particular species might persist only until the growing season commences and the seeds are exposed to the correct conditions for dormancy-break and germination. A small proportion of seeds could end up in different micro-sites (where conditions for dormancy-break and germination did not occur) and persist for longer time periods. A relatively large variance around the mean of these persistence times might indicate that persistence varied due to deterministic impacts of external conditions or seed traits, or could be interpreted as evidence of stochastic variation in persistence (see later sections of this article). Regardless of the magnitude of variance of persistence, and the causal mechanisms underlying these patterns in seed survival, we intend to make it clear that without such measures of seed persistence, we cannot hope to properly incorporate this crucial plant trait alongside other indicators of plant response to their environment.

Many seed- and soil-related factors are variable both within sites and between years, and therefore we concur with Long et al (2015) that there is a continuum of response with respect to seed persistence. We also add that this response is variable both amongst and within species, and that this requires the expression of seed persistence as a mean with associated variance, but also that seed persistence is explicitly communicated as a response to a defined set of conditions. We suggest that multivariate regression techniques are used to determine the relative importance of different factors in explaining seed persistence such as (but not limited to) those factors reviewed by Long et al (2015). The explicit link between seed persistence and the surrounding environment allows extrapolation to other situations and can be incorporated into a larger trait-level database. This would enable ecologists to confidently identify known persistence times for species of interest, or failing this, identify species with similar traits and judge whether estimates of seed persistence can be transferred and used in lieu of empirical data.

The limited utility of seed persistence definitions in ecological research

Whilst ecological research has failed to adequately incorporate seed persistence into theoretical or empirical studies, ecologists are not entirely at fault because the existing literature on seed persistence is surprisingly indiscriminate with regards to the endpoint of persistence – seed persistence is defined as seed survival "from the time they reach maturity on the parent plant until they germinate, are eaten or decayed, or age and die” (Long et al 2015). However, the distinction between the two outcomes of germination *versus* seed death is critical to whether persistence is contributing to population growth in the case of germination, or population decline if seeds die. If certain conditions reliably cause death, seed banks could not contribute to maintaining or increasing population growth rate and therefore fall outside of the species’ niche. Conversely, a germinated seed indicates that the individual plant has made it through the constraints of post-dispersal survival to enter the regeneration phase, and has a chance to reproduce assuming that the conditions characterising the niche at various subsequent life stages continues to be met. So the current definition of persistence that ends with germination or seed death are of limited use for ecological research because they allow persistence to be classified regardless of the outcome; for example, the entirely opposing scenarios of 100% germination or 100% seed death within a few years would both be classed as short-term persistent. Given that the relative proportion of death or germination over the long-term defines whether the environment supports a source or sink population, the conflation of seed death and germination is a major barrier to understanding the niche of plants and consequently prevents the design of effective conservation management programmes (Sutherland et al., 2006).

Determining whether seed persistence ends in death or germination also has implications for the accuracy of estimations of persistence times. If a seed's existence in the soil ends with germination, then the seed *may* have persisted for longer had suitable germination conditions not arrived, and in this case, potential seed persistence until death will be underestimated. To illustrate this point further, we highlight the seedbank duration data originally presented in the LEDA Traitbase (Kleyer et al., 2008) and made available through the TRY Plant Trait Database version 4.1 as Trait ID 2809 (Kattge et al., 2011). The complete dataset reported contains 38929 observations of seedbank duration (in months) for 1549 species (n varies from 1 to 439 observations per species; Figure 2). Each observation actually reports the time period after dispersal or deliberate burial, to the point when seeds were sampled from the soil and successfully germinated. The reporting of seedbank duration is potentially problematic because each reported observation is the time at which the seeds were sampled and germinated, and not the potential longevity of the seeds. There is no capacity to report sampling that did not result in germination, i.e. the point at which seeds may all be dead. Whilst the LEDA and TRY databases provide accompanying materials to explain this, it appears that errors of analysis and interpretation may occur if researchers conflate this data with the accepted definition of seed persistence as ending in germination or death. Figure 3 provides a visualisation of how these data might be communicated – mean seedbank duration is the arithmetic mean of all observations per species and maximum duration of the seedbank is the longest time period since seed burial reported for each species. Mean seedbank duration is flawed because it implies an average survival when it is actually the average time period for which seeds were buried and then dug up and germinated. Maximum seedbank duration is more useful because it gives an indication of the potential seed persistence, but cannot be linked to the many factors affecting seed survival detailed in this and previous contributions (e.g. Long et al 2015). The reporting of seedbank duration as the point at which seeds were deliberately germinated can confirm that the seedbank is still viable but cannot convey for how much longer the seedbank might last.

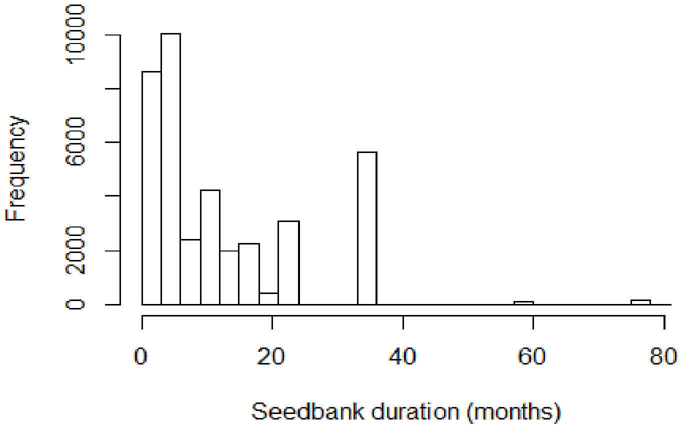

Figure 2. Seedbank duration data (months) for all data as reported in the TRY Trait Database (Kattge et al. 2011)

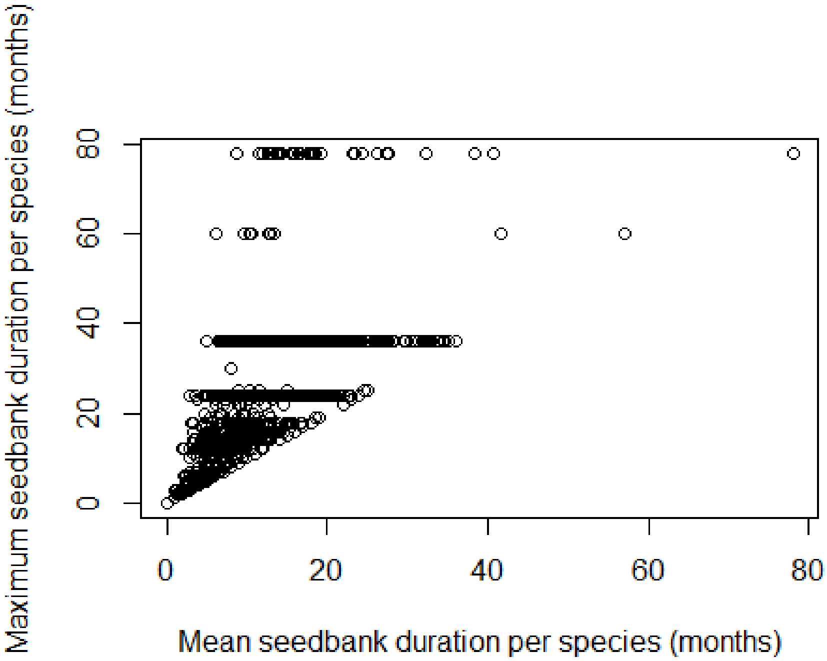

Figure 3. Seedbank duration reported in the LEDA traitbase (and available through TRY database, see text for details) expressed as mean duration (months) per species against

maximum reported duration (months) for the same species. Replication varies considerably (n = 1 - 439 observations) per species.

The seedbank duration data presented in LEDA and TRY trait databases are an affirmation that the seeds are still present and viable, but cannot convey actual persistence. This is akin to measuring plant height regularly in the first few months-years of a plants life and expressing that as the final plant height when actually the plant survives for many more years and attains heights of 30 or 40 m. The difference of course is that we can see how tall a seedling might be by visual comparison with mature examples surrounding it, but we can’t see the seed bank or trace the age without complicated methods (see above). Whilst seed researchers may recognise this problem to be a property of the data necessitated by the methods available to us, the wider plant ecology community might not, and would erroneously use these data with other traits to look at broader ecological questions.

What is important is seed persistence until death, and what conditions cause death, because these data allow us to build persistence decay curves that are tied to particular conditions. Whilst monitoring seeds in their post-dispersal phase is extremely complicated, this does not mean that measuring seed persistence is an impossible task. Although it is unfeasible to determine the persistence ability of each seed dispersed from a plant, efforts should be channeled to understand seed persistence at community level and comparisons on relevant ecosystems and co-existing ability with other species.

Niche theory and the importance of seed persistence

Niche theory is around a century old (Wake et al., 2009) but producing accurate niche descriptions has taken on renewed relevance with applications in niche modelling, evolutionary biology, functional and community ecology, climate change science and paleoecology (Blonder, 2017). In the following sections we aim to highlight different roles that seed persistence contributes in improving niche descriptions of plants and moving ecological science further towards being a predictive discipline.

Seed persistence is necessary to define the metapopulation niche

Where niche descriptions omit the role of seed banks in population persistence, the logical outcome of temporary habitat unsuitability is population extinction, at least until immigration can restore the population to that site. Whilst for animals this accurately explains metapopulation dynamics, the description is inadequate for plants with a seed bank that can persist through unsuitable growing conditions. Therefore, to describe the requirements of the entire metapopulation, it is necessary to know the time periods over which seeds can typically persist in different microhabitats in order to accurately define the species' or metapopulation niche. Determining what is the appropriate time scale over which to describe the conditions required to meet the species' niche draws parallels with Pulliam's (2000) theoretical treatment of spatial dispersal: seed dispersal through space needs to be properly defined relative to the scale of habitat patchiness to understand the difference between the realized and fundamental niches – unoccupied suitable patches may be falsely assumed to be unsuitable unless dispersal limitation is well-defined. Similarly, seeds may disperse through time by persisting in the soil but unless the persistence time is long enough to coincide with suitable conditions for germination or growth, the seeds will die. In other words, metapopulation niches have to be temporally- as well as spatially-explicit to allow for proper predictions of metapopulation survival.

Seed persistence has not been adequately integrated into population growth definitions

Seed persistence has been incorporated in population growth models such as those by Chesson (1994) which defined population growth of annual plant species as a function of environmental suitability, and incorporated seed survival rate as the survival of seeds that do not germinate during a defined time period over which the population growth rate was calculated. By incorporating a temporal component, allowing for the existence of a seed bank and distinguishing between seed death and germination Chesson's (1994) seed bank model presents our most complete treatment of plant population dynamics. However, a number of refinements need to be made to accurately represent the known properties of post-dispersal seed 'behaviour'.

Firstly, seed survival rate is assumed to be constant but this is likely to change depending on the age of the seeds (Valleriani and Tielbörger, 2006), and will also change depending on environmental conditions experienced by the seeds in the soil or other pressures impacting upon seeds (see supplementary data). As long as the aboveground population’s niche requirements are met, the age of the seeds is apparently not important for understanding population survival, but has significant implications where the vegetation fails to regenerate or recruit as seed persistence will become the mechanism by which the population might recover. However, the relative contribution of seeds from different cohorts is impossible to discern based purely on in-soil abundance which is a measure often relied upon to describe the seed bank of a species, and regular inputs will mask the relative contribution of seeds that are of older cohorts. Therefore, to properly describe population growth, the survival of seeds of differing ages needs to be better understood.

In situations where the aboveground vegetation has entirely died out, the shape of the survival decay curve following the last input of seeds not only defines how long there might be a viable seed bank, it also dictates whether it is likely that viable seeds will be present in enough numbers to enable population recovery should suitable conditions return. Seed survival in *ex situ* storage (i.e. in cool, dry conditions) generally follows a normally distributed sigmoid curve if all the seeds in a sample are viable at the point of being stored (Mead and Gray, 1999). But *in situ* persistence may vary and consequently, seed survival rates used in population projections must account for a variability depending on the shape of the mortality curves and the abundance of seeds in the soil relative to the last input of seeds from the parent plant community.

Seed persistence contributes to both stochastic and deterministic components of the niche

We can safely assume that there are several, and possibly very many, parameters that determine seed persistence. However, seed survival in the soil is not an entirely deterministic phenomenon and drawing further on the parallels between temporal seed persistence and spatial propagule dispersal suggests that there will be a strong stochastic component to seed persistence. As a consequence of this stochasticity, it is tempting to disregard seed persistence as a critical part of the species' niche especially given that seed persistence may be a weaker filter of population survival compared to other life stages where deterministic niche requirements are narrower. However, separating the proportion of seed persistence variability that is simply stochastic, from that which is deterministic, is key to not only predict expected seed persistence, but also, the typical *variation* in persistence times under specified conditions. The stochastic element of seed survival in the soil has the potential to contribute to niche theory by forming a mechanism that might acknowledge the roles of both deterministic niche theory and neutral theory in explaining patterns of occurrence.

Another implication of the existence of stochasticity in seed persistence is the survival of the metapopulation. Where several populations in a locality, a metapopulation, respond deterministically to the same conditions, we might expect that these populations have a high level of synchrony within scales that those deterministic variables operate (Liebhold et al., 2004). Population synchrony is associated with higher extinction risk because events causing mortality at landscape or regional scales are likely to affect all populations equally severely and leads to loss of the metapopulation as a whole. Consequently, metapopulation survival is promoted by an optimal level of asynchrony between subpopulations (Heino et al., 1997; Lande et al., 2003) and given that seed persistence is potentially an important source of demographic stochasticity, it is likely to contribute to avoiding local extinctions by reducing population synchrony.

Careful experimentation can uncover some of the explanatory variables of persistence but cannot represent the many different influential conditions that seeds are subjected to. Additionally, study duration is generally too short to encompass long persistence times. To address this constraint, distinguishing deterministic from stochastic processes can be achieved by understanding if species' distributions respond to environmental gradients, or if neutral models of stochastic processes can be assumed to explain distribution patterns (Chase and Myers, 2011). Whilst deterministic responses are either already described, or relatively easy to describe, for aboveground vegetation, the response in terms of seed persistence relies on advances in describing the seed persistence niche to discern where environmental tolerances lie and how they might impact upon species response to environmental change.

Applications and further research

Understanding seed persistence in soil has many ecological applications, and thus, failure to predict which species might persist in different microenvironments hampers our ability to model population dynamics and manage focal species and communities. For example, inaccurate seed persistence predictions may lead to i) misapplied and costly weed management, ii) the failure of threatened species reintroductions in environments with high interannual variation where a seed bank is key to survival, iii) the unanticipated release of an invasive species from regeneration constraints, iv) the restoration of vegetation that is less diverse and functionally inferior than the original community, and v) erroneous predictions of plant community response as climate change progresses. Below we outline some practical suggestions that we hope to further the study of seed persistence and integration of this important trait with other aspects of plant biology.

(1) Focus on species that are declining

Whilst it is impossible to describe the persistence ability of 350,000 angiosperm species, it is pragmatic to prioritise which species should form the basis of study. Previous investigations have estimated persistence ability of seeds for various purposes, not limited to, but including ecological restoration, community ecology, threatened plant conservation, species distribution and community co-existence, weed management, seed pathogens effect, seed loss via soil erosion, responses to changes in flooding and the impacts of subterranean animals on soil seed banks. These studies are essential, but we propose that estimating persistence of declining species should be prioritized, especially those showing negative responses to recent climate change. A decline in abundance indicates that the species no longer occupies its niche space, either for germination or growth and/or the space of the realised niche has become smaller. This may have resulted from changing climate, species competition, change in soil properties or seasonal change. Targeting these species might inform the critical role of seed persistence in species that are demonstrably vulnerable to environmental changes.

(2) Determine persistence using more than one method

Given that the methods available to estimate soil seed persistence carry limitations, a combined approach tailored to the species in question is recommended. For example, if soil-core extraction had shown that seeds of a particular species can be found at various depths, then artificially burying the seeds to all the possible depths and estimating the viability is an appropriate method for exploring persistence variation. The critical question of how long the artificial burial experiments must be conducted requires careful thought. Current categorization of seed-banks limits the duration of studies to 5 years, and experimental work typically reports this at one depth. Our alternative suggestion of using various depths based on soil-core exhumation, informs the longevity of seeds in the soil at different micro-climates occurring at different depths. Thus, efforts should be channeled to bury the seeds for longer than 5 years to determine longevity with seed extraction every 3 months during first two years and annually after that until 5 years and biannually after that until 90% of the seeds have died or germinated. In addition to germination experiments, methods such as tetrazolium test could be incorporated to distinguish whether the seeds have died or remain viable. Also, we suggest burying seeds at several locations, as seeds can disperse and consequently be exposed to different, and maybe even novel, micro-conditions.

(3) Distinguishing persistence and longevity of seeds in the soil

Although we acknowledge that proportions of germinating seed are often reported as affirmation of survival to a specified time point, and in the best examples, viability testing is used to discern mortality of seeds in the ungerminated proportion, there is still confusion with regards to the end point of persistence that has the potential to make definitions unworkable. For example, in Long et al (2015), seed persistence is defined as "The survival of seeds from the time they reach maturity on the parent plant until they germinate, are eaten or decayed, or age and die." (see Table 1, p.35 of Long et al. 2015). So whilst we know that seed ecologists do indeed know the difference between seed death and germination, for seed traits to be incorporated into other analyses, particularly large trait-based studies, we think that definitions need to be made more specific. To this end, we recommend that seed persistence is reported with respect to a defined end point, and this may be germination, predation or other destruction, whilst seed longevity is reserved for persistence until death (whether this is in situ or ex situ).

(4) Incorporate seed traits into persistence estimation

Saatkamp et al. (2018) lists the following traits that contribute to persistence: seed size, seed mass, germination speed, seed metabolic rate, serotiny, seed coat thickness, dispersal potential, response to chemical cues, seed nutrient content, seasonality of seed release, seed coat permeability, seed shape, seed defense, seed defenses, longevity. In addition to this, we note that dispersal structures, ability to remain attached to covering structures, e.g. pods, ability to withstand drying, i.e. orthodox or recalcitrant, germination requirement, e.g. light/dark or appropriate temperature might also play crucial role in determining the entry and exit of seeds in the soil. Incorporating these traits into persistence estimation could likely inform what species might become extinct and appropriate conservation plans to be developed. To this end, the literature on seed persistence contains some generalizable theories on what traits confer persistence. For example, seeds with impermeable coats show higher ability to persist in soil, whereas seeds that are desiccation-sensitive, i.e. recalcitrant germinate or die immediately after dispersal and therefore persist in soil for a maximum of few months (Baskin and Baskin, 2014). However, relationships between persistence and other seed traits are not so straightforward. Thus, much information is required at community level and our knowledge gap raises further questions that can be only answered with further studies:

(a) What are the additional seed traits that drive seed persistence?
(b) Do plants in different life-forms differ in seed persistence?
(c) Is there a relationship between ecosystem functioning and seed persistence ability?
(d) What are the large-scale phylogenetic patterns of seed persistence?

Concluding remarks

Every aspect of climate, seed position, potential for dormancy, time since dispersal, pathogen loadings, seed predation, seed morphology and soil characteristics can interact positively and negatively to result in variation in seed persistence even amongst individuals of the same species. For this reason, the factors influencing soil seed persistence can be conceptualized as a multi-dimensional hyperspace similar to those constructed to describe a plant's niche, and the awareness that different factors may shift in their relative importance depending on timing and environment is similarly appropriate. When a particular species is studied by including all the seed and soil related parameters that are known to affect persistence, it would become apparent that a continuum of response might exist with all seeds germinating soon after dispersal in one set of conditions and most seeds persisting for long time periods in another set of conditions. We strongly recommend that these parameters are included in species-level niche descriptions and that our insights into the importance of deterministic factors affecting persistence, and the potential for demographic stochasticity to be introduced as a result of variable seed persistence, are exposed to a wide spectrum of researchers of plant ecology. The inclusion of seed persistence in niche descriptions will be an important step in moving ecology and niche theory from descriptive to predictive (Gewin, 2006) over 100 years since niche concept emerged (Wake et al 2009), and 40 years since Grubb's inception of the regeneration niche (Grubb 1977). Given that our environment is a dynamic and shifting system, categorizations of seed persistence cannot convey the variation in response to a seed's environment and a more nuanced understanding of seed persistence embracing our perception of soil seed survival as a 'continuum' is necessary to understand and predict species and community response, and protect our ecological systems under global environmental change.

Conflict of interest

None.

Authors contribution

GKJ and SED contributed equally to the development of ideas and writing. GB and JK maintain TRY-database, provided the data for analysis presented in figures 2 and 3 and helped with revision. We also sincerely thank two anonymous reviewers, especially one reviewer during revision, for their constructive comments on an earlier version of the manuscript.

Supplementary Data

Table 1. Important factors known to affect the entry and exit of seeds in the soil.

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