Ensuring the availability of adequate seed supplies of species and sources appropriate for restoration projects and programs necessitates extensive science-based planning. The selection of target species requires a review of disturbance conditions and reference areas, development of a reference model, and consideration of specific objectives, timeframes, available resources, and budgets as well as the performance of prospective species in past restoration efforts. Identification of seed sources adapted to site conditions is critical to provide for short-term establishment and long-term sustainability. Seed zones and plant movement guidelines provide tools for sourcing plant materials with reduced risk of maladaptation. A seed zone framework also facilitates seed use planning and contributes to stability and predictability of the commercial market, thereby reducing costs and improving the availability of adapted seed supplies. Calculating the amount of seed required for each species is based on seed quality (viability, purity), seed weight, expected seedling establishment, and desired composition of the seeding. If adequate collections from wildland stands are not feasible, then seed increase in seed fields or use of nursery stock may be warranted. Adherence to seed collection and seed production protocols for conserving genetic diversity is critical to protect genetic resources and buffer new seedings and plantings against environmental stressors. Maintenance of genetic diversity becomes even more critical considering current or expected climate change impacts. Collaboration and partnerships can benefit seed selection and procurement programs through sharing of information, coordination in project planning, and increasing the availability of native seed.

**Key words:** climate change, direct seeding, genetic diversity, native seed needs assessment, native seed procurement, seed zones, workhorse species

**Implications for Practice**

- Early planning for seed needs based on site evaluation and examination of reference areas enables procurement of adequate quantities of seed of adapted species and seed sources.
- Seed zone maps and related tools, where available, can aid in selecting seed sources and lower the risk of maladaptation.
- Maintaining genetic diversity from seed collection through field increase and planting is crucial for reducing the risk of project failure.
- Seed source selection and management practices to maintain diversity and adaptive capacity are critical for effective response to climate change.
- Coordination of short- and long-term seed procurement needs improves availability of necessary seed sources.

**Introduction**

Early planning for future seed needs is essential for ensuring that sufficient quantities of the appropriate species and provenances will be available for restoration projects and programs when and where it is needed. Depending on the plant species, source requirements, quantities desired, and method of procurement, it can take 3 years or more (Fig. 1, from Armstrong et al. 2017) to acquire the target amount of plant material. A missed window of seed harvesting can result in delays of several years due to seed crop periodicity, and unpredictable weather and other factors. It becomes all the more important to determine seed needs for planned projects (e.g. roadside revegetation, pollinator and other wildlife habitat enhancement, invasive weed management), and for emergency restoration needs when there is a high likelihood of unplanned disturbances such as wildfires or flooding. This article focuses on considerations for determining seed requirements for individual projects as well as multi-year, larger-scale needs for a specific planning area (e.g. seed zones

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Native species will be most successful in achieving climate effectiveness (e.g. increased abundance and diversity of plant communities, as well as options for procuring needed quantities of seeds of the desired species and sources.

**Seed Need Planning**

The selection of target species for a particular planting project or seed planning area can depend on management needs and timeframes, as well as strategies or initiatives that emphasize specific objectives such as pollinator habitat enhancement, erosion control, or protection of at-risk species. Development of a reference model and selection of reference sites may provide useful guidance for establishing restoration goals and evaluating progress toward meeting those goals (see Gann et al. 2019). Reference models may include historical records of plant communities or species assemblages at contemporary reference sites. In situations where it would be extremely challenging to return ecosystems to historical conditions and ecological trajectories, reference models may be adapted to guide restoration to new target conditions and to accommodate ongoing transformations caused by climate change and other disturbances (Hiers et al. 2012; Armstrong et al. 2017; Gann et al. 2019).

Key environmental factors to consider when designing seed mixes include local temperature and moisture regimes, soil conditions, species abundance, and where applicable, successional status. Planting a diversity of species and life forms (e.g. annual and perennial grass and forb species, shrubs, trees, nitrogen fixers, wetland species, species with overlapping and sequential bloom periods) appropriate to current or anticipated future environmental conditions is generally desirable (Whisenant 1999; Dion et al. 2017) and may improve treatment effectiveness (e.g. increased abundance and diversity of pollinator visitations), resilience to disturbances such as climate change, and resistance to invasive plant encroachment (Norland et al. 2015). Data and resources for evaluating which native species will be most successful in achieving management objectives for a particular project or seed banking program include:

- Comprehensive plant surveys of project sites, and nearby reference areas with similar environmental conditions or that approximate anticipated future climates or post-disturbance trajectory of highly disturbed or altered sites (e.g. increased sunlight and temperatures, reduced water availability, invasive plant competition, altered soil conditions, etc.) (Gann et al. 2019).
- Local botanical experts.
- Nursery managers and seed producers.
- Plant propagation manuals and online resources.
- Herbarium and historical records.
- Literature, online tools, and applications describing local flora and plant communities.
- GIS analytical tools and databases that identify suitable species for local areas (e.g. Ecoregional Revegetation Application, http://www.nativerevegetation.org/era/) or that map species distributions for current and projected future climates (e.g. Species Habitat Tool, https://specieshabitattool.org/spht/).

Other important factors to consider when selecting restoration species, especially when large quantities of plant materials are required, are the extent of wildland stands, the cost and ease of wildland seed collection, plant performance and seed production capabilities in nursery and agronomic environments, and availability of appropriate sources in the commercial market (Atkinson et al. 2018). Commonly used restoration species are often referred to as “workhorse” species (Erickson 2008). These are species that establish and thrive in a wide range of sites and ecological settings, often with little assistance from irrigation or fertilizer. Developing seed sources for native species with unknown or poorly understood propagation requirements is likely to increase costs and require longer timeframes. Despite these constraints, more specialized species may still receive emphasis if they fulfill a desired ecological function or management objective (e.g. host plants for pollinators), are culturally important, or are needed for projects containing unique microclimates or soils types (e.g. wetlands/riparian areas, serpentine soils).

**Quantity of Seed Required for Direct Seeding**

The total amount of seed required for a restoration project or seed planning area is dependent on the projected restoration acreage, the desired plant density of each target species, and key physical and biological seed attributes such as germination and seed purity percentages and the number of seeds per kilogram. Additional reserves for contingency seedings may be required if site resource or environmental conditions are expected to adversely affect seedling survival. For many grass and forb species, seed is applied directly on project sites. If appropriate seed is unavailable in the commercial market or if wildland seed collections are inadequate for direct use, seed may first be grown in nurseries or seed-increase fields where plants can be cultured and harvested to produce larger quantities.

![Seed planning, sourcing, and procurement](image-url)
of seed. Plants may be maintained for a period of one to several years depending on the species and projected seed needs. Field-grown seeds can then be planted directly in project sites or stored for future use in warehouses or freezers.

For each restoration project or seed planning area, the amount of seed required can be calculated as shown in Table 1 for western pearly everlasting (Anaphalis margaritacea) (Armstrong et al. 2017; NRCS 2019). Depending on the quantities required and the timeframe of the needs, the seeds may be wildland collected or obtained through establishment of seed-increase fields.

### Table 1

Calculation of pure live seed required for a direct seeding project. Note: Purity and germination can be derived using information contained in Pedrini and Dixon (2020) and The Royal Botanic Gardens, Kew Seed Information Database (SID) (RBG Kew 2019).

| A | Number of seeds/kg<sup>a</sup> | 17,640,000 seeds/kg |
|---|-----------------------------|---------------------|
| B | Purity<sup>a</sup>          | 60%                 |
| C | Germination<sup>a</sup>     | 85%                 |
| D | A * (B/100) * (C/100)       | 9,000,000 PLS/kg    |
| E | Field survival              | 3%                  |
| F | Target seedling density     | 269 seedlings/m²     |
| G | Target composition          | 10%                 |
| H | (F * E) * G =               | 893 PLS/m²          |
| I | (1,000 * H)/D               | 1 kg/ha             |
| J | Area to seed                | 10 ha               |
| K | I * J =                     | 10 kg               |

<sup>a</sup>Available data for the species. Certified seed laboratory results for the seed lot should be used for project calculations when available.

### Quantity of Seed Needed for Establishing Seed Increase Fields

Seed increase fields may be established if appropriate sources are unavailable in the commercial market or if seed demand is greater than what can feasibly or economically be met within the required timeframe through wildland collections. Table 2 (Armstrong et al. 2017) provides an example of the steps involved and the information required for determining the amount of wild seed to provide a grower in order to produce the desired amount of seed. More precise guidance can be obtained directly from the seed producer because sowing rates, seed yields, and production timeframes can vary greatly depending on grower location, cultural and harvesting practices, and experience with the target species. In nearly all cases, the wildland seed provided to a grower should be tested at a certified seed testing laboratory, if available, to determine important attributes such as seed germination/viability, the number of seeds per kilogram, seed purity, and the amount of nontarget or noxious weed species.

The quantity of wild seed collected in a single year is frequently inadequate for establishing a seed-increase field. In these situations, one option is to store seed and make additional collections across multiple years until a sufficient amount of seed is available for field establishment. Another approach is to sow a small plot of wildland seed, and then harvest the first-generation seed to establish a larger seed increase field. Small collections may also be first sown in a nursery (e.g. in pots circa 16–33 cm<sup>3</sup> in size), and then transplanted into a seed production field at low densities (<3 seedlings per meter). This strategy reduces the overall amount of wild seed needed for field establishment as well as the time to first harvest. The fields may also be more productive than direct sown fields because the plants are evenly spaced and larger.

### Quantity of Seed Needed for Nursery Seedling Production

Successful restoration of many tree and shrub species often requires the use of planting stock with established root systems, especially in areas with heavy grazing pressure or on harsh or disturbed sites such as roadsides. In these circumstances, seeds (or vegetative cuttings) are grown for several months or years in nursery beds or greenhouses. A variety of stocktypes are used, from barefoot and container seedlings that can be produced in less than 1 year, to larger transplanted containerized stock that have a longer production cycle but greater survival and growth in stressful environments due to their larger size. Sedges (Carex spp.), rushes (Juncus spp.), and many other wetland taxa are often collected and propagated using both seed and seedling production strategies.

The amount of seeds needed to produce a target number of "shippable" (acceptable) seedlings in a nursery is determined by seed germination and purity percentages, the number of seeds per kilogram, and the nursery factor. If seed testing results are not available, approximations of germination, purity, and seeds per kilogram can be obtained from published references, seed bank databases, and seed laboratory and extractory managers. The nursery factor for estimating the proportion of viable seeds that will produce "shippable" seedlings is based on nursery experience and culturing practices. For more difficult-to-grow species, nursery factors may be less than 50%. Nursery factors for target species as well as guidance on the quantity of seed needed to meet the seedling order can be obtained from nursery managers.
Table 2 Calculation of pure live seed required for establishment of seed increase fields.

|    | Description                                                                 |
|----|-----------------------------------------------------------------------------|
| A  | Seed production needs                                                      10 kg |
| B  | Years in production                                                        2 years |
| C  | Sowing rates                                                                1.1 kg/ha |
| D  | Annual seed yields                                                         56 kg ha yr⁻¹ |
| E  | A/B/D                                                                      0.09 ha |
| F  | E * C =                                                                    0.1 kg |
| G  | Cleaned-to-rough-cleaned seed ratio                                        33% |
| H  | 100/G * F                                                                 0.3 kg |

The amount of seed needed to produce a target number of “shippable” seedlings can be estimated using the following equation (Armstrong et al. 2017):

Quantity of seedlings needed: [(% germ/100) * (% purity/100) * (seeds/kg) * (nursery factor/100)].

Seed Sourcing

Selection of genetically appropriate seed sources is crucial for effective and responsible restoration, both in the short and long term. If plant materials are poorly matched to local site and environmental conditions, projects may fail or be unsustainable over time due to poor regeneration potential, genetic degradation, disrupted plant–pollinator relationships, or loss of resiliency and adaptive capacity in coping with environmental stressors such as invasive plants and climate change (Hufford & Mazer 2003; Broadhurst et al. 2008; Bischoff et al. 2010; Havens et al. 2015; Bucharova 2017). Having knowledge of seed origin and the genetic diversity and background of available plant material is an important first step for ensuring adapted and resilient plant populations.

Although seed of local origin or provenance is generally considered to have the greatest adaptive potential (McKay et al. 2005; Crémieux et al. 2010; Mijnsbrugge et al. 2010), genetic research indicates that geographic distance is generally a poor predictor of adaptive differentiation (Leimu & Fischer 2008; Richardson et al. 2015). This means there is no fixed distance or rule of thumb for determining where plant material may be successfully moved from its site of origin. Instead, “local” is best defined by the climate and environmental similarity of the source material relative to the planting site where it will be transferred (Hufford & Mazer 2003; Savolainen et al. 2004; Johnson et al. 2010).

Maintaining Adaptive Capacity: Seed Zones and Transfer Guidelines

Plant adaptation is influenced by a wide array of climatic and environmental factors such as precipitation, aridity, temperature, aspect, and soil characteristics. The degree of adaptation may vary greatly among species, from genetic generalists that can abide broad movement across environmental gradients to genetic specialists that are more tightly adapted to local conditions and regions (Rehfeldt 1994; Johnson et al. 2010). Common garden experiments and reciprocal transplant studies are empirical approaches for investigating species-specific adaptive strategies and patterns of genetic variation in a given geographic area (e.g. Campbell 1986; Sorensen 1992). In these studies, variation in important adaptive traits involving survival, growth, and fecundity is correlated to climate and environmental variables of the plant sources included in the experiment. The results can then be used to create species-specific seed transfer guidelines and delineate discrete regions of similar environments (seed zones) within which plant materials can be moved with little risk of maladaptation at new planting locations (Fig. 2). Seed zones have a long history in forestry, especially in the United States and Europe, but have only recently been developed for herbaceous species used in restoration (e.g. Erickson et al. 2004; Homing et al. 2008; Johnson et al. 2013; St. Clair et al. 2013; Bower et al. 2014; Bucharova 2017; Durka et al. 2017). New online tools such as SeedZone Mapper (https://www.fs.fed.us/wwetac/threatmap/TRMSeedZoneData.php) have been developed to catalogue

Figure 2 Species-specific seed zones for: (A) Douglas-fir (Pseudotsuga menziesii, a genetic specialist) and (B) western red cedar (Thuja plicata, a genetic generalist) in western Oregon, U.S.A. The size and configuration of the seed zones for the two species reflect differing patterns of adaptive genetic variation across the landscape, as determined from common garden studies. Seed zones for genetic specialists like Douglas-fir are much smaller, with more restrictive seed movement relative to western red cedar and other generalist species that can tolerate broad movement with little risk of maladaptation.
available seed zone information and allow end-users to view and download GIS data for further use in seed collection and restoration planning.

In addition to enhancing restoration outcomes, seed zones can generate efficiencies and economy of scale in seed and plant production systems, as well as stability and predictability in the commercial market. A seed zone framework greatly facilitates seed use planning and creates opportunities for the sharing and exchange of plant material among land owners and seed banking programs and partners. Collectively these attributes help reduce plant material and overall restoration costs, leading to the increased availability and use of genetically appropriate plant materials in restoration. In spite of the many benefits, seed zones are generally lacking for many herbaceous species required in restoration. In these cases, ecoregional approaches that delineate land areas encompassing similar geology, climate, soils, hydrology and vegetation or other geographic descriptors may be useful proxies for directing seed movement and the collection and sourcing of plant materials. In the United States, generalized provisional seed zones (Bower et al. 2014) have been developed using climate data (winter minimum temperature and aridity) along with ecoregional boundaries to delineate areas that have similar climates but differ ecologically. The provisional zones serve as a useful starting point for ensuring adaptability and protecting genetic resources, especially when used in conjunction with species-specific genetic and ecological information in addition to local knowledge. The ecoregional approach has also been utilized in several European countries, including Austria, Czech Republic, France, Germany, and Switzerland (Fig. 3) (De Vitis & St. Clair 2018).

Maintaining Genetic Diversity

An additional important concern in native plant material development and use regards the sampling and maintenance of genetic diversity. All phases of seed and plant production, from wild collection, processing, grow-out, and harvesting, should employ methods that conserve inherent genetic diversity. This will not only protect genetic resources, but also help improve initial restoration success and provide resiliency against environmental pressures and changing conditions in the future (Rogers & Montalvo 2004; Basey et al. 2015). In addition, the restored population must include a sufficient number of unrelated parents to minimize the potential for adverse impacts due to inbreeding. Restoration practitioners should be mindful of genetic diversity needs and concerns whether they are purchasing plant materials or collecting and propagating their own sources. When seed is purchased in the commercial market, the most suitable plant material for a particular project can be assessed through review of government websites and published literature and by consultations with reputable seed producers and brokers. Important factors to consider include seed origin and certification class (if available). In the United States, many of the more recent native species germplasm releases are certified as “Source Identified” to indicate that no selection or genetic modification has occurred in the original wildland parent population or in subsequent generations grown in seed-increase fields or seed production areas and orchards (Young et al. 2003).

Although no single protocol for plant material collection and propagation is guaranteed to safeguard genetic integrity in all situations, following are some general guidelines for consideration when purchasing or collecting/growing seed and seedlings (adapted from Armstrong et al. 2017; see also Rogers & Montalvo 2004; Basey et al. 2015):

**Number of unrelated parents.** Collecting seed or cuttings from 50 or more unrelated parent plants is often recommended as a general guideline for obtaining a representative sampling of genetic diversity in a population. A similar amount of seed or cuttings should be collected from each plant. If parental contributions are unequal, a larger number of parent plants should be sampled to increase diversity. When collecting cuttings for vegetative propagation of dioecious species, practitioners should strive for a balanced male–female ratio to ensure that both sexes are adequately represented in the collection.

**Number of collection sites.** Collecting seeds or cuttings from multiple areas within a seed zone will help provide a representative sampling of among-population genetic diversity. Ideally, collection sites would span the full range of environmental and climatic conditions within a seed zone or management area. An approximately equal number of parents should be sampled...
within each area. Collecting material from larger populations and avoidance of isolated, fragmented stands where inbreeding or past genetic bottlenecks may reduce genetic diversity are other sampling strategies that can enhance genetic diversity. **Individual parents within a collection site.** To reduce the risk of collecting from related individuals (e.g., siblings or clones of the same plant), seed and cuttings should be obtained from plants that are well separated from one another (Vekemans & Hardy 2004; Rhodes et al. 2014). Genetic diversity and representation can also be improved by collecting from plants well dispersed throughout the collection site. In outcrossing species, an important consideration for maintaining genetic diversity is to avoid collecting from isolated plants that may have reduced opportunity for cross-pollination with a wide array of pollen donors. Other recommendations for safeguarding genetic integrity and diversity include collecting plant material throughout the entire flowering period and avoiding inadvertent selection that could result in a disproportionate representation of certain plant types (e.g., earlier flowering, larger sized, or heavier seed producers).

After seed collection, a number of cultural practices and biases in subsequent stages of the plant production cycle can also potentially affect the genetic integrity and diversity of the source material (Schroder & Prasse 2013). Following are some of the more obvious situations to avoid or minimize:

- Bias in selecting seed or plants for crop establishment based on their size or morphology.
- Irrigation, fertilization, or cultural practices that favor certain plant types, causing artificial selection (e.g., trait shifts or reductions in the diversity of the population).
- Harvesting practices that favor certain phenotypes through timing, frequency, or type of harvest method (hand, mechanical).
- Intentional or unintentional removal of viable seed during the seed cleaning process (e.g., seed sizing, grading large seed from small, selection based on seed color).
- Seed storage conditions that cause loss of viable seeds over time (e.g., large fluctuations in temperature or humidity).

Mixing seed crops from different harvest years or re-collecting wild sources on an ongoing basis for establishment of new production fields are other effective strategies for guarding against the degradation of genetic diversity in native plant materials and restored populations.

**Seed Sourcing for Changing Climates**

For many regions of the world, changing climates will require plant populations to rapidly respond to new environmental conditions and pressures, including habitat alteration and fragmentation, precipitation and temperature extremes, uncharacteristic wildfires, stresses from invasive plant species, and new and intensifying insect and disease infestations. Seeding and planting will become increasingly important tools for mitigating these impacts, and for re-aligning species and populations to keep pace with changing climates and altered disturbance regimes. Although some species and populations may be more vulnerable to climate change (Fig. 4) and the specific effects are highly context dependent (Hufford & Mazer 2003; Broadhurst et al. 2008; St. Clair & Howe 2011), resiliency, diversity, and adaptability will remain overarching strategies for sourcing plant materials for future climates. Methods that enhance diversity, such as the use of diverse species and seed sources and creation of structural diversity within stands and across landscapes, are crucial safeguards for ensuring successful restoration in both the short and long term. Other important objectives are the maintenance of large populations with high connectivity to promote gene flow of adapted genes (via seed and pollen) in the direction of trending climates (e.g., lower to higher latitude or elevation changes). Maintaining and sharing accurate records of plant material sources, combined with well-designed monitoring strategies, will be essential for informing and adjusting restoration practices over time.

Many plant populations are already growing outside their optimal climate as a result of environmental changes that have outpaced the rate of species’ response capabilities (adapta- tional lag, Aitken et al. 2008; Gray & Hamann 2013). In these situations, seed sourcing protocols may be modified to shift emphasis from using only seed from local sources to selecting seed (or a portion of the seed) based on similarities with projected future climate or to climate changes that have already occurred in the recent past. Matching seed sources to climates is made more feasible by the advent of GIS mapping programs that use existing data and climate projections to predict which seed sources will be best adapted to a given planting site, or which planting sites will be most suitable for a given seed source. In North America, the Seedlot Selection Tool (Fig. 5) (https://seedlotselctiontool.org/sst) and the Climate Smart Restoration Tool (climatorestorationtool.org/csr/) are becoming widely used for tree and shrub/herbaceous species, respectively. A similar application, ResTOOL, is available for plant material selection and restoration of tropical dry forests in Columbia (http://www.restool.org/en/index.php).

“Climate smart” seed sourcing strategies based on near-term climate projections (e.g., 10–20 year planning horizon) will reduce the uncertainty and risk associated with reliance on climate projections for the more distant future. This will also promote the use of plant material that will be optimally adapted to environmental conditions during the highly vulnerable early stages of seed and seedling establishment. For many geographic regions, the direction of plant movement for changing climates will be from the warmer, drier environments of lower latitudes and elevations to higher latitudes and elevations where conditions are cooler and wetter. Flexibility in creating custom seedlots for future climates is greatly facilitated by protocols that collect and bulk seedlots across a narrow range of environments (e.g., temperature or precipitation bands).

**Seed Procurement**

Once the species, sources, and quantities of seed required for a specific project or long-term program have been determined, procurement strategies and plans must be carefully developed.
Several options are available, and decisions require consideration of funding, timelines, and available resources. Some plant materials may be immediately available (off-the-shelf purchases, seed in storage), whereas acquisition of others can require several years depending upon the seed sources selected and time requirements for wildland collection or agricultural seed production. Where available, seed certification and testing standards help to strengthen procurement plans. Common types of procurement tools used for acquiring seed from collectors and seed producers are described in Pedrini et al. (2020).

Improving Seed Availability Through Collaboration and Partnerships

Seed procurement and banking programs are likely to be most successful and cost effective if managers are able to coordinate and prioritize multi-year seed needs in conjunction with other resource disciplines, agencies, and landowners within a seed planning area (seed zone or other biogeographic area). This more integrated and comprehensive approach to seed planning can benefit a wide range of resource needs, protect against over-harvesting, and lead to an increased availability of native seed when and where it is most urgently needed for restoring disturbed sites and ecosystems. Other critical factors affecting seed planning and procurement success include supporting infrastructure such as proper storage facilities (warehouse, freezer), seed processing facilities, and nurseries, as well as seed producers who can operate at a scale appropriate to the production needs of the clients. While not “seed need planning” per se, access to supporting infrastructure is essential for successful native plant material programs and remains a serious constraint to planning efforts and seed supplies in many areas. In these cases, partnerships and careful coordination become all the more important in providing for needs through the creation of opportunities to share in planning costs, infrastructure investments, and native seed production.

Conclusions

Successful seedings and seed programs rely on early and thorough planning to identify seed needs. Examination of a comprehensive site evaluation, reference areas in various stages of recovery, and other available resources aid in identifying seed needs for individual projects. Species selected to meet restoration goals should have a history of use in restoration, but some specialist species may be essential and require research or the attention of a skilled propagator. Appropriate sources for each species are selected using available seed zone maps or related tools along with knowledge of the species ecology and potential response to climate change. The species, sources, and quantity of seed required can then be incorporated into the scheduling and budgeting processes early on as 2–3 years may be required.
to obtain some seed sources. Procurement of appropriate plant materials may require wildland collection and in some cases increase in agricultural seed fields or nurseries. Collection and increase should follow established protocols and guidelines to obtain and maintain maximal genetic diversity and fitness to improve the resistance and resilience of restored communities.

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