Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: Insights from a global survey

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Abstract
Meeting the multimillion hectare commitments for forest and landscape restoration (FLR) will require billions of tree seed and seedlings. However, the adequacy of seed supply in terms of quantity, genetic diversity and quality has received scant attention in FLR planning. We surveyed 139 FLR projects worldwide and identified widespread problems in the availability and diversity of tree seed, with potentially deleterious consequences for the vigor, productivity and long-term persistence of restored tree populations. Large projects and those focused on climate change mitigation were particularly associated with multiple problems in seed sourcing. To avoid large-scale failure in FLR, we recommend: (1) national assessments of seed supply and demand for FLR, (2) reviewing FLR targets and funding cycles, (3) fostering sharing of knowledge and experiences regarding seed supply and selection, (4) enhancing seed exchange across landscapes, and (5) introducing regulations for seed quality and strengthening capacities for compliance.

KEYWORDS
climate change mitigation, genetic diversity, local adaptation, multiple correspondence analysis, tree seed supply

1 INTRODUCTION

All forest and landscape restoration (FLR) projects require access to land and seed. The need to consider the biophysical and political dimensions of land during restoration planning is broadly recognized. The 13th Conference of Parties to the UN Convention on Biological Diversity emphasized the need to review legal and policy frameworks for land tenure and establish spatial planning processes to create an enabling environment for restoration (CBD, 2016). By contrast, the quality, availability of, and access to tree seed has received little attention in high-level policy and planning. Yet, restoring just a million hectares of degraded forest land—a fraction of recent unprecedented global restoration commitments—can easily require a billion seedlings (Broadhurst, Jones, Smith, North, & Guja, 2016; New York Declaration on Forests, 2014; United Nations, 2015). What these seedlings are, where they come from, how they are selected, produced and delivered and by whom, are neither trivial nor merely technical issues for FLR to be effective and provide expected benefits.

The number of species used in FLR projects may vary broadly, depending on their availability and each project’s ecological and socioeconomic objectives (Jalonen et al., 2014). Nevertheless, genetic diversity is vital for all FLR. Returns on investments in FLR depend directly on the genetic diversity and origin of the seed used, as these influence...
germination, seedling growth and survival, productivity, seed set, resistance to pests and diseases and capacity to adapt to environmental change (Aguilar, Ashworth, Galetto, & Aizen, 2006; Alfaro et al., 2014; Broadhurst, North, & Young, 2006; Graudal et al., 2014). Yet, the few genetic studies in restored forests suggest that restoration practitioners lack awareness of the importance of genetic diversity: projects often use seed that is either not adapted to the planting site or has strongly reduced diversity with collection from very few parent trees (Boziano et al., 2014; Broadhurst, 2013; Liu, Chen, Zhang, & Shen, 2008; Navasques & Emerson, 2007).

The scale of current global FLR commitments is likely to attract new restoration practitioners, seed producers and suppliers, many of who lack experience in producing or selecting seed effectively to help meet restoration objectives. As demand for tree seed grows rapidly, limited attention to seed production and delivery in restoration planning suggest that supply is lagging (Broadhurst et al., 2016). Simultaneously, continued habitat loss and fragmentation reduce the availability of seed sources and their genetic diversity (Vranckx, Jacquemyn, Muys, & Honnay, 2012). In this dynamic environment, it is increasingly unlikely that national restoration targets can be met without coordinated efforts to improve the quality, quantity and diversity of tree seed and its accessibility to practitioners.

To identify options for strengthening tree seed production and delivery systems to meet national and global FLR commitments, we surveyed seed sourcing practices in FLR projects worldwide. We assessed (i) from where and how tree seed was sourced for 139 projects; (ii) what problems practitioners perceive in seed availability and (iii) how those problems affect project implementation. We highlight genetic diversity, resulting from different seed sourcing strategies, as a limiting factor in how likely FLR projects are to succeed in establishing functional, self-sustaining ecosystems. We identify widespread problems in seed production and delivery that constrain achievement of FLR targets, and discuss policy options to overcome these.

‘Seed’ is used in this article as a generic term to refer to different types of forest reproductive material such as seed, seedlings and vegetatively propagated material.

2 | METHODS

We conducted a survey during October–November 2015, targeting practitioners who had been involved in the selection, collection, or purchase of propagation material for FLR projects. Practitioners were asked to respond with reference to the latest project on which they were, or had been, working, and where planting or seeding had occurred. The questionnaire consisted of multiple-choice and open-ended questions and was available in English, French, Russian, and Spanish (S1). The survey was administered mainly electronically and distributed through websites and email-lists of international and regional forest and conservation organizations (S2).

Survey responses were analyzed using Multiple Correspondence Analysis (MCA; LeRoux & Rouanet, 2010). A multidimensional space was constructed using the responses to 12 multiple-choice questions on project purpose, design and seed sourcing strategies (active variables), to analyze which response options contributed most to the variance in response patterns and which options were associated. Response options were grouped into two to six categories per question, resulting in 42 active categories. Importance of axes was evaluated using cumulated modified rates of variance. Each axis in the multidimensional space was interpreted using categories that had greater than average contribution to that axis. Responses to the remaining survey questions (e.g., frequency of problems in seed sourcing, consideration of climate change) and derived information (e.g., country income status; World Bank, 2015) were used as supplementary categories that did not contribute to construction of the multidimensional space but were then projected onto it to study whether any categories clustered in specific parts of the space. The analysis was performed using “soc.ca” package (Grau Larsen, Ellersgaard, & Andrade, 2016) in R software version 3.2.2 (R Core Team, 2013).

3 | RESULTS

Respondents described seed sourcing strategies of 139 FLR projects in 57 countries (Table 1, S3 & S4). Most respondents had a background in forestry (42%) or environmental sciences (15%); 68% had a postgraduate degree, while 66% had been involved in FLR for at least 5 years. Most respondents (91%) had been directly involved in the selection or collection of propagation material for the projects they described.

Cumulated modified rates of variance of the first five axes in MCA were 33%, 52%, 66%, 77%, and 85%. We interpret the first three axes. The 21 categories selected for interpreting axis 1 represent 86% of its variance, showing a gradient from decentralized (A1–) to centralized (A1+) project implementation and seed sourcing strategies (Table 2, S5). The 16 categories for interpreting axis 2 represent 78% of its variance, with a gradient from small-scale (<10 ha), knowledge-intensive projects that apply at least some seed selection criteria (A2–), to large-scale projects (>500 ha) focusing on carbon sequestration or timber production and lacking seed selection criteria (A2+). Axis 3 (12 categories represent 77% of its variance) separates projects by size and main restoration method (tree planting, A3–, vs. assisted natural regeneration, A3+), while indicating that large-scale projects aiming at restoring species-rich forests are often associated with using
## Table 1  Characteristics of the surveyed forest and landscape restoration projects by region

|                     | Global | Africa | Asia | Latin America | Australia, Europe and North America |
|---------------------|--------|--------|------|---------------|-------------------------------------|
| **Responses**       | 139    | 31     | 54   | 42            | 12                                  |
| **Countries**       | 57     | 21     | 19   | 13            | 7                                   |

**Purpose (mode, % projects)**

|                     | Global | Africa | Asia | Latin America | Australia, Europe and North America |
|---------------------|--------|--------|------|---------------|-------------------------------------|
| **Main purpose**    |        |        |      |               |                                     |
| Habitat restoration (52%) |        |        |      |               |                                     |
| **Secondary purpose** |        |        |      |               |                                     |
| Species conservation (29%) |        |        |      |               |                                     |
| Carbon sequestration (27%) |        |        |      |               |                                     |
| Food production (32%) |        |        |      |               |                                     |
| **Project leader (% projects)** |        |        |      |               |                                     |
| Government organization | 36%    | 33%    | 53% | 23%           | 41%                                 |
| Academic or research organization | 33%    | 27%    | 34% | 40%           | 33%                                 |
| Local civil society organization | 28%    | 40%    | 26% | 38%           | 25%                                 |
| **Area (median category, ha)** | 51–100 | 51–100 | 101–500 | 11–30 | 31–50 |
| **No. of tree species used (median category)** | 6–10 | 11–20 | 6–10 | 6–10 | 6–10 |
| **Proportion of native species (median category)** | >95% | 81–95% | >95% | >95% | >95% |
| **Year when project started (median)** | 2010 | 2009 | 2011 | 2008 | 2009 |
| **Years between project inception and inception of planting or sowing (mean)** | 1.2 | 1.7 | 1.1 | 1.0 | 1.1 |
| **Duration of project at the time of responding (mean, years)** | 6.4 | 7.1 | 5.9 | 6.4 | 6.2 |
| **Projects completed by the time of responding (%)** | 49% | 65% | 35% | 52% | 50% |

*Includes the 12 responses from Australia, Europe, and United States of America.
†Estimated as 0.5 years if within the same calendar year.

Most projects that used natural regeneration as the main source were of small area (≤10 ha) surrounded by reportedly abundant seed sources (≥50 parent trees per species; A3+).

Seed sources were selected primarily on the source’s proximity to the restoration site (defined by respondents as within 1–300 km; median 10 km) (Fig. 2). The similarity of current environmental conditions between the seed source and restoration site was considered a criterion for seed source selection in 65% of projects. Although 40% of respondents opined that forests used as seed sources were often degraded or fragmented (Fig. 3a), avoiding such sources was considered a selection criterion in only 29% of projects and seldom as the most important criterion (Fig. 2).

In total 56% of projects used at least some population-level criteria to help ensure the collection of genetically diverse seed, such as specifying a minimum number of seed trees (29% of projects; defined as from one to 400–600 trees, mode and median 10 trees), a minimum distance between seed...
TABLE 2  Main response categories explaining variance in response patterns, identified using Multiple Correspondence Analysis. Categories on one side of an axis (+ or −) tend to be associated with each other and oppose categories on the opposite side of the axis. Only categories contributing more than the average to any of the three first axes (100%/42 categories = 2.38%) are shown. Categories selected for the interpretation of an axis are in bold font.

| Variable and categories | Coordinates | Contribution to the axis variance (%) |
|-------------------------|-------------|----------------------------------------|
|                         | Axis 1 | Axis 2 | Axis 3 | Axis 1 | Axis 2 | Axis 3 |
| **Project characteristics** |   |   |   |   |   |   |
| **Leader**              |   |   |   |   |   |   |
| Academic or research organization | −0.38 | −0.57 | 0.37 | 1.4 | 3.7 | 1.7 |
| Government organization  | 0.57  | −0.16 | −0.14 | 3   | 0.3  | 0.2  |
| Local civil society organization | −0.59 | 0.42  | −0.03 | 2.6 | 1.5  | 0.0  |
| **Main purpose**        |   |   |   |   |   |   |
| Timber production        | 0.98  | 1.09  | −0.03 | 4.1 | 5.9  | 0.0  |
| Carbon sequestration     | 0.58  | 1.64  | 0.34  | 0.5 | 4.8  | 0.2  |
| Production of NTFP       | 1.05  | −0.76 | 0.43  | 3.4 | 2.0  | 0.7  |
| Other ecosystem services | 0.36  | −0.1  | 1.61  | 0.4 | 0.0  | 10.9 |
| Habitat restoration      | −0.42 | −0.19 | −0.33 | 4.3 | 1.0  | 3.2  |
| **Area**                |   |   |   |   |   |   |
| Large (>500 ha)          | 0.65  | 0.75  | −0.55 | 4.9 | 7.5  | 4.4  |
| Medium (11–500 ha)       | −0.39 | −0.03 | 0.09  | 2.7 | 0.0  | 0.2  |
| Small (≤10 ha)           | −0.05 | −0.76 | 0.51  | 0   | 7.3  | 3.6  |
| **Number of species**    |   |   |   |   |   |   |
| Few (≤10)                | 0.44  | −0.27 | 0.2   | 3.6 | 1.6  | 0.9  |
| Numerous (>50)           | −0.43 | 0.48  | −0.83 | 1.1 | 1.6  | 5.3  |
| **Native species**       |   |   |   |   |   |   |
| Exclusively (>95%)       | −0.31 | 0.14  | −0.15 | 2.6 | 0.7  | 0.8  |
| Minority (<50%)          | 0.76  | −0.25 | 0.37  | 6.8 | 0.8  | 2.0  |
| **Propagation material** |   |   |   |   |   |   |
| Natural regeneration     | 0.31  | 1.57  | 1.4   | 0.3 | 9.6  | 8.3  |
| Wildlings                | −0.85 | 0.13  | 0.39  | 3.9 | 0.1  | 1.1  |
| Nursery seedlings        | 0.08  | −0.19 | −0.28 | 0.2 | 1.0  | 2.5  |
| **Main supplier**        |   |   |   |   |   |   |
| Academic or research organization | 0.52 | −0.85 | −0.19 | 1   | 3.1  | 0.2  |
| Community-based nursery  | −0.91 | 0.79  | −0.68 | 3   | 2.7  | 2.1  |
| Forestry department      | 1.1   | 0.45  | −0.14 | 9.3 | 1.8  | 0.2  |
| Natural regeneration     | −0.46 | 0.97  | 2.65  | 0.5 | 2.7  | 21.8 |
| **Main source**          |   |   |   |   |   |   |
| Natural Forest           | −0.45 | −0.04 | −0.06 | 5.5 | 0.0  | 0.1  |
| Seed orchard             | 1.11  | −0.89 | 0.5   | 5.7 | 4.2  | 1.4  |
| Restored or planted forest| 0.88 | 0.69  | 0.37  | 4.7 | 3.4  | 1.0  |
| Seed production area     | 1.07  | 0.5   | −1.16 | 2.8 | 0.7  | 4.2  |
| **Number of seed trees** |   |   |   |   |   |   |
| Moderate (6–15)          | −0.32 | −0.67 | −0.17 | 0.7 | 3.6  | 0.3  |
| Few (≤5)                 | 0.1   | −0.17 | −0.74 | 0.1 | 0.2  | 4.7  |
| Sufficient (>15)         | 0.24  | −0.35 | 0.53  | 0.6 | 1.4  | 3.8  |
| **Seed selection criteria** |   |   |   |   |   |   |
| **Main criterion for seed source** |   |   |   |   |   |   |
| Ease of accessibility    | 0.69  | 0.45  | −0.58 | 2.2 | 1.1  | 2.0  |

(Continues)
trees (21%) or avoiding collecting seed from isolated trees (15%). Such criteria were associated with projects involving academic or research organizations as project leaders or seed suppliers, or sourcing material from seed orchards (A2–). Lack of any population-level criteria was associated with large projects aimed at timber production or carbon sequestration, reliance on natural regeneration, and sourcing from community-based nurseries or restored or planted forests (A2+). The number of seed trees per species was known to respondents in 49% of projects. Half of them indicated that seed was from more than 15 trees, while 28% said the seed was from five or fewer trees. Using very few seed trees was associated with large-scale projects aimed at restoring species-rich forests through planting nursery seedlings (A3–).

In total 32% of respondents indicated that their project considered climate change when planning from where or how to source seed. Such considerations were commonest among projects that involved academic or research organizations and applied at least some population-level criteria in seed selection, but least common in projects that focused on timber production or carbon sequestration, or lacked seed selection criteria (A2– vs. A2+). Seventeen percent of respondents could identify specific project strategies to strengthen the adaptive capacity of the restored tree populations in the face of changing climate. These strategies were mainly aimed at increasing the diversity of species or selecting species with specific functional traits (8% of respondents). Only two respondents (1%) explained that their projects tried to increase genetic diversity through more extensive germplasm collection.

According to respondents, 78% of projects often experienced problems obtaining seed from seed markets and 65% had problems finding suitable seed sources. The most common market-related problems were an overall lack of planting material (54% of projects), a lack of material of preferred provenance or origin (58%) and material of unknown provenance or origin (50%) (Fig. 3a). Specific problems mentioned repeatedly in open-ended responses included many nurseries growing only commercially important species (15 mentions), difficulty in obtaining information about seed collection practices (8), lack of seed collection criteria at commercial nurseries (6), lack of competition between seed suppliers, contributing to high prices without guaranteeing carefully selected seed (6), and generally low market prices for tree seedlings, which doesn't motivate nurseries to focus on quality (3). Other than market-related problems, open-ended responses also included: the difficulty of finding seed sources often led to collecting from few seed trees (13 mentions); irregular seed production (5); short viability of recalcitrant seeds (4); and poor propagation success in nurseries (4). Problems in obtaining propagation material often resulted in higher costs (47% of respondents), using fewer species than planned (42%) and delays (41%) (Fig. 3b). Problems did not cluster along the main MCA axes but were spread across the multidimensional space (S7), indicating that projects with diverse characteristics and seed sourcing strategies experienced similar problems with the availability of seed sources and seed markets. Seventy-six percent of respondents suggested approaches to help improve seed supply to FLR projects (open-ended question). Among them, 24% suggested technical improvements such as research on propagation methods, 24% suggested focusing increasingly on decentralized seed production approaches (e.g., projects collecting their own seed or working with community-based nurseries), while 21% proposed working with multiple actors and strengthening both decentralized and centralized seed sourcing strategies.

### Discussion

Although the number of survey responses covers a small portion of FLR projects worldwide, our results offer the first global overview of problems in the supply and selection of tree seed for FLR. These problems can profoundly affect restoration success but have received little attention (Bozzano et al., 2014; Broadhurst et al., 2006; Kettenring, Mercer,
Reinhardt Adams, & Hines, 2014). It is difficult to estimate the representativeness of the sample as global statistics on FLR projects are not available. However, the described projects represent a wide range of implementers, locations, sizes, ages, and seed sourcing strategies, indicating the survey reached a wide variety of respondents.

Our results indicate that lack of sufficiently diverse tree seed is a widespread problem in FLR projects and programmes worldwide, commonly causing delays and increasing project costs—and above all, constraining the achievement of restoration objectives. Seed supply networks are underdeveloped, with a majority of projects collecting at least part of their seed themselves, mostly from nearby natural forests. On one hand, these choices appear related to a frequent failure of tree seed markets to meet practitioners’ preferences for species and provenances, or their expectations for product quality. On the other hand, restoration practitioners themselves commonly lack capacity in seed selection, as indicated by the lack of seed collection guidelines in projects, selection of seed sources primarily based on geographical distance from the restoration site, and overlooking the impacts of climate change. The widespread view that it is preferable to use nearby seed sources because of local adaptation in trees at very small scales (typically ≤10 km in this study) has little support from research (e.g., Boshier et al., 2015; Gellie, Breed, Thurgate, Kennedy, & Lowe, 2016; Kettenring et al., 2014; McKay, Christian, Harrison, & Rice, 2005). Restoration projects that aimed at mitigating climate change emerged as having particularly poor seed sourcing practices. This is alarming in light of the importance given to forest-based mitigation and adaptation in international climate policy (UNFCCC, 2015), as is the low genetic diversity associated with projects for restoring species-rich forests.

Currently, the lack of awareness of the importance of seed genetic quality among restoration practitioners results in limited demand, and probably willingness to pay a premium for seed collected using existing scientific criteria to guarantee genetic diversity. Even government-led tree planting programmes may choose to purchase seedlings primarily based on price, which incentivizes mass production of low quality seedlings (Dedefo, Derero, Tesfaye, & Muriuki, 2017; Gregorio, Herbohn, Harrison, Pasa, & Ferraren, 2017). Government bodies or nongovernmental organizations may supply free seedlings, often of unknown quality, to boost tree planting (Lillesø et al., 2011). Under such conditions, it is unlikely that existing seed supply networks could rapidly evolve through self-regulation to produce genetically more

**FIGURE 1** Main seed sourcing strategies from global survey of tree seed sourcing practices in forest restoration projects, % of all projects: (a) main supplier of propagation material, (b) main type of propagation material, (c) main source of propagation material

**FIGURE 2** Main criterion in selecting seed source populations in forest and landscape restoration projects

environ. conditions similar to predicted future conditions on target site 3% not degraded or fragmented 2%

close to target site 51%

easy to access 13%

environ. conditions similar to target site 31%
diverse seed. In the short term, it is more likely that the lack of seed in markets will drive restoration practitioners towards establishing project nurseries. Collection from restored or planted forests is emerging as the most important secondary seed sourcing strategy. As such forests may often have been established from seed with narrow genetic diversity, using them as seed sources risks cascading genetic bottleneck effects, with negative impacts of inbreeding accumulating over successive tree generations (Lengkeek, Jaenicke, & Dawson, 2005; Reed & Frankham, 2003).

We recommend the following policy interventions to increase the use of genetically diverse seed in FLR and improve the likelihood of establishing functional restored forest ecosystems:

1. **Conduct national assessments of seed supply and demand for meeting FLR targets.** Gaps in seed supply and strategies to address them can effectively be identified only if analyzed beyond the project-level. It is noteworthy that the need for strengthening seed production capacities emerged as important in almost all the 30 countries where IUCN and World Resources Institute recently conducted national assessments of restoration opportunities (ROAM) (M. Kuzee, pers. comm). Seed supply assessments need to consider quantity, genetic quality and geographical origin of seed sources, for example, the size, population status and distribution of existing seed production areas for target species across eco-geographical zones, in relation to projected demand. Supra-national assessments could be useful for species of interest to several countries.

2. **Review FLR targets and funding cycles.** Given the long life cycles of trees, building seed supply to meet the demand from FLR typically takes years. Overly ambitious FLR targets and short funding cycles can result in selecting species and seed sources based on what is readily available rather than what best meets project objectives (Stanturf et al., 2015). Early steps towards implementing FLR targets should include specific investments in enhancing the availability of and access to quality seed where seed supply for target species is inadequate. Initial performance of FLR projects and programmes must be assessed using not only quantitative (e.g., numbers of seedlings planted) but also qualitative indicators (e.g., strategies used for sourcing seed).

3. **Foster sharing of knowledge and experiences of seed selection and supply options.** There is no previous experience in producing and delivering tree seed at the scale needed to meet global FLR commitments. It is important to accelerate learning of which approaches work and which don't for different species and socioeconomic contexts, and what roles different actors can play in the process (Lillesø et al., 2017). Multistakeholder platforms that bring together restoration practitioners, seed suppliers, policy makers and other stakeholders can help identify seed production and delivery models and test and evaluate these in diverse environments. Functional platforms for broader FLR-related topics already exist in some countries and regions and could be built upon (Melo et al., 2013).

4. **Facilitate seed exchange across landscapes.** Practitioners’ perceptions about the distances over which tree seed can be safely transferred need to be broadened, to shift the focus in seed collection from the nearest available sources to those that are genetically viable. Effective mechanisms for sharing information about seed sources, transporting seed and documenting its provenance are also needed. Using multiple seed sourcing strategies, such as engaging with independent collectors, community-based organizations and seed exchange programmes, has been shown to yield more diversity (measured by number of species and seed lots) than relying on any single strategy (Brancalion, Viani, Aronson, Rodrigues, & Nave, 2012). Seed enterprises need to access broader markets to remain
economically viable (Graudal & Lillesø, 2007), so creating mechanisms that help connect seed suppliers with buyers across landscapes can bring both ecological and socioeconomic benefits. A growing number of studies also recommend expanding the range of seed sources and stimulating gene flow by restoring landscape connectivity to help forests adapt under changing environments (e.g., Breed, Stead, Ottewell, Gardner, & Lowe, 2013; Prober et al., 2015; Sgrò, Lowe, & Hoffmann, 2011)—something that, our results suggest, very few practitioners currently consider. Practical guidelines and tools for “climate-smart” FLR are needed (see www.restool.org), but developing them requires research to understand patterns of adaptive genetic diversity in target species (Whittet, Cottrell, Cavers, Pecurul, & Ennos, 2016).

5. Establish regulations on seed quality and strengthen capacities for compliance. Few countries have regulations on tree seed markets, or successfully enforce them (Gregorio et al., 2017; Nyoka et al., 2015). Accreditation of seed sources and nurseries can be an important step towards ensuring the use of more diverse seed of documented provenance. Accreditation should be a process for strengthening capacities and monitoring progress, rather than simply certifying those who meet preset requirements. Local entrepreneurs, nongovernmental and community-based organizations can benefit from job and income opportunities associated with seed production, but need support to achieve accreditation and access seed markets (Gregorio et al., 2017; Lillesø et al. 2017). Project funding should be used to strengthen such supply systems where they exist, instead of relying on extensive self-collection (Roshetko et al., 2017). Requirements to use only accredited seed in publicly funded FLR projects and programmes should be introduced as the supply of such seed grows. Parties implementing and funding climate-focused FLR projects and programmes should urgently adopt, and monitor compliance with, guidelines on seed diversity and provenance, as a condition to funding.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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