Research Article

Land-Cover Legacy Effects on Arbuscular Mycorrhizal Abundance in Human and Wildlife Dominated Systems in Tropical Savanna

Geoffrey E. Soka¹ and Mark E. Ritchie²

¹Department of Wildlife Management, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania
²Department of Biology, Syracuse University, New York, NY 13244, USA

Correspondence should be addressed to Geoffrey E. Soka; gesoka@gmail.com

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Arbuscular mycorrhizal fungi (AMF) can be important mutualists to plant hosts in acquiring soil nutrients. Past work has not explored whether previous land-cover history influences current AMF abundance in croplands and whether different land-cover histories in grazed but not cultivated areas influence AMF. This study was conducted to assess the effects of land-cover history in and near Serengeti National Park on AMF abundance in areas with three different land uses. The results showed that land-cover history influenced a number of soil physicochemical properties following conversion of grassland to cropland or woodland to cropland during the past 27 years. Different original land cover generally did not significantly influence current AMF abundance in croplands or livestock-grazed soils. However, livestock-grazed current grasslands that were formerly woodlands had lower AMF abundance than sites that had been grasslands since 1984. These results suggest that lower AMF abundance in livestock-grazed and cropland areas as compared to protected wildlife-grazed areas may reflect reduced total carbon inputs and higher disturbance and are not strongly influenced by the legacy of previous land cover. Given that recent studies have detected legacy effects on AMF, such effects may reflect more the impact on the taxonomic composition of AMF rather than their total abundance.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are ubiquitous soil fungi, forming mutualistic symbiosis with a majority of terrestrial plant species [1–3]. AMF are promising candidates for universal indicators of land management legacies and soil quality degradation [4–6]. The connection between land-use legacies and AMF abundance has been a subject of great interest to the scientific community. Legacy effects of land-use changes have been considered among the most influential disturbances affecting diversity, community structure, and ecosystem functioning and services of microbial communities [7, 8]. Legacy effects occur when the presence of previous vegetation or land use alters soil properties or organism species pools in ways that persist even if the previous vegetation is changed due to succession, deliberate conversion, or restoration [8–12]. For example, land-use changes have been found to alter the soil characteristics and aboveground species dynamics [13–16] and consequently influence microbial community structure and function [16–20]. A chronosequence study along successional gradient has shown that microbial communities tend to become more similar to those in native soils over time [21]. However, residual influence of prior conversion to agriculture has been observed in microbial communities even many years after restoration of forests after agricultural cultivation [22–24].

Soils often continued to reflect their history of previous vegetation and disturbance for many years, through persistent changes in soil chemical and structural properties [7, 9, 25, 26]. For example, historical farming in tropic region has resulted in higher soil phosphorous contents and lower soil carbon and nitrogen contents compared to sites with a long continuity of forest cover [9, 27, 28]. Because microbial adaptation and recovery may play a significant
role in ecosystem responses to human impacts [29–33], the long-term consequences of past land-use decisions on soil microbial communities are crucial for predicting current and future ecosystem functioning and services [18, 34]. While many studies have found that microbial communities differ in response to land-use legacy [15, 21, 35–40], there is poor understanding of the association between land-use history and the abundance of AMF in tropical soils.

To help understand the association between land-cover history and soil microbes, the abundance of AMF associated with different land-cover histories in and near the Serengeti was compared. There are three main land uses in the Serengeti region: protected area wildlife-grazed savannas, uncultivated open areas used for livestock grazing, and cultivated fields. Consequently, there are different land-cover histories for each land use, such as transitions from grassland to woodland versus persistent woodland, transition from savanna woodland to grassland versus persistent grassland, or recent conversion of woodland or grassland to cultivation versus persistent cultivation. These land-cover transitions are potentially associated with different soil properties, such as extractable P, total soil N, and pH. For example, grasslands recently arising from loss of woodland may have higher residual N or P in organic matter compared to grasslands that have not recently converted from woodland [41]. Such residual differences among different land-use histories could influence AMF abundance, as a prior study in the Serengeti region [41] found that soil properties varied among different land uses and explained significant variation in AMF hyphal densities. Consequently, AM hyphal abundance was hypothesized to be more strongly influenced by current land-use and less associated with land-cover history because of physical soil disturbance from tillage and reduction in host plant biomass and potentially C inputs in livestock-grazed sites.

In this study, land-cover classifications of 1984 and 2011 Landsat imagery were used to determine histories for 112 sites in the Serengeti region that were currently (in 2011) in one of the three major land uses. AMF abundance was sampled from multiple soil cores at each site, along with several hypothetically important soil properties, such as extractable P, total soil N, and pH. The association of AMF abundance with land-cover histories for each of the different land uses was determined with ANCOVA to search for influences of land-use histories independent of current differences in soil properties. This paper has significant potential in helping to shape our understanding of the abundance and dynamics of AMF in soils under different land-use/cover classes.

2. Materials and Methods

2.1. Study Site Description. Samples were collected inside (wildlife-grazed) Serengeti National Park (SNP), Tanzania, in East Africa (34°–36°E longitude and 1°–2°S latitude, Figure 1) and on adjacent open lands that were used either for livestock grazing (livestock grazed) or for cultivated crops (croplands). The area lies approximately about 240 km south of the equator, resulting in a fairly constant mean monthly temperature and an annual change of only 4–6°C [42]. The ecosystem is characterized by a bimodal rainfall pattern, with the short rains occurring typically from November to December, the long rains usually taking place between March and May, and a long dry season from June to October. The southeastern Serengeti consists of C₄-grass dominated grasslands that shift from short to medium to tallgrass plains towards the north and westward [43]. The northern and western parts of the Serengeti consist predominantly of Acacia woodlands punctuated by large patches of open C₄ grassland. This wide variety in vegetation types allows the Serengeti to support over 30 species of ungulates numbering close to 3 million individuals, including 2 million migratory wildebeest (Connochaetes taurinus), zebra (Equus burchelli), and Thomson’s gazelles (Gazella thomsonii) that impose the majority of grazing impact [44] which averages 63% of aboveground biomass each year [43].

The land-use system in and near Serengeti comprises natural woodlands and grasslands inside and outside the park and croplands outside the park. Natural woodland and grassland inside the park are characterized by minimal wildlife grazing intensities while woodland and grassland outside the park are characterized by heavy grazing intensities associated with overgrazing (by cattle) and other human related activities such as charcoal burning, cutting of trees for timber, fire wood, and harvesting of nontimber products. Livestock (mostly cattle but with some sheep and goats) are maintained at relatively high densities sufficient to consume 70–90% of aboveground biomass (McSherry and Ritchie in preparation). Agricultural systems outside the park comprise small-scale subsistence varieties (Zea mays and Phaseolus

Figure 1: Map of study sites and location of study area within Tanzania.
Table 1: Brief description of land-use/cover classes in and near SNP.

| Land use/cover | Location | Management       | Description                                                                 |
|---------------|----------|------------------|------------------------------------------------------------------------------|
| Grassland in  | Inside SNP Protected area | Herbaceous vegetation generally below 2 m including grasses and sedges for wildlife conservation. Fully protected with strict conservation measures. Areas covered by natural trees (single-stem woody plants generally taller than 1.5 m at densities <50% canopy cover) for wildlife conservation. Fully protected with strict conservation measures. Includes areas used for annual crop cultivation. |
| Woodland in   | Inside SNP Protected area | Areas covered by trees (single-stem woody plants generally taller than 1.5 m at densities <50% canopy cover) used for communal grazing. |
| Cultivated land | Outside SNP Private land | Includes areas used for annual crop cultivation. maize-bean intercropping system characterized by low inorganic inputs (an estimate of 30 kg P and N/ha) combined with farm yard manure. |
| Grassland out | Outside SNP Public land | Herbaceous vegetation generally below 2 m including grasses and sedges used for communal grazing. |
| Woodland out  | Outside SNP Public land | Represents areas covered by trees (single-stem woody plants generally taller than 1.5 m at densities <50% canopy cover) used for communal grazing. |

Table 2: Remotely sensed data used in the analysis of land-use/cover change in and near SNP.

| Sensor          | Acquisition date | Image ID                  | Path/row | Season |
|-----------------|------------------|---------------------------|----------|--------|
| Landsat TM      | August 1984      | LT5169061A984047XXX02     | 169/61   | Dry    |
| Landsat TM      | August 1984      | LT5169062A984183XXX08     | 169/62   | Dry    |
| Landsat TM      | August 1984      | LT5170061A984366XXX01     | 170/61   | Dry    |
| Landsat TM      | August 1984      | LT5170062A984188XXX01     | 170/62   | Dry    |
| Landsat TM and ETM+ | August 2011 | LT5169062A2011087MLK00   | 169/61   | Dry    |
| Landsat TM and ETM+ | August 2011 | LT5169062A2011087MLK00   | 169/62   | Dry    |
| Landsat TM and ETM+ | August 2011 | LT5170062A2011084MLK01   | 170/61   | Dry    |
| Landsat TM and ETM+ | August 2011 | LT5170062A2011084MLK01   | 170/62   | Dry    |

Note. TM: thematic mapper; ETM+: enhanced thematic mapper plus.

vulgaris) grown with applications of external inorganic fertilizer inputs (estimate of 30 kg nitrogen and phosphorus per hectare combined with farm yard manure) (Table 1).

2.2. Field Soil Sampling and Soil Laboratory Analyses. The effects of land use/cover changes on AM hyphal abundance across 112 sites (20 × 20 m plot) in the Serengeti region (Figure 1) were studied. Field soil sampling and soil laboratory analyses are detailed in Soka et al. [41]. The extraction and determination of AM hyphal abundance from soils which were collected at each site are summarized in Soka et al. [41]. Soil pH, total nitrogen (N), and available phosphorus (P) were measured at each site to determine how these soil properties were associated with land-cover changes.

2.3. Remote Sensing Data Collection

2.3.1. Image Selection, Acquisition, and Analysis. Spatial patterns of land use/cover changes using remote sensing data (1984–2011) derived from the satellite imagery to determine the influence of land-cover history on AM hyphal abundance were established. Landsat 5 TM and 7 ETM+ cloud-free with spatial resolution of 30 m for the Greater Serengeti were acquired from the U.S. Geological Survey (USGS) archive (http://earthexplorer.usgs.gov/). Landsat imagery was selected because it is readily and freely available and frequently used for land-cover classification [45]. The dates were determined by image availability and were paired relatively close in time to help ensure consistency in cover classes and phenology (Table 2). The image processing and classification were performed using the topographical map and land-use map obtained from Tanzania Wildlife Research Institute (TAWIRI). These maps were also used to conduct ground observations to verify the classification results from satellite imagery (Figure 2). To ensure accurate identification of land-cover changes and geometric compatibility with other sources of information, the images were geometrically corrected using a 1:50000 scale topographical map and resampled to a local Tanzania UTM coordinate system in UTM zone 36 south of the equator in which Serengeti is located. The images were georeferenced in WGS84 system, UTM zone 36S.

Atmospheric correction was performed to remove the effects of the atmosphere on the reflectance values of images. In order to reinforce visual interpretability of images, a colour composite (Landsat TM bands 3, 4, and 5) was prepared based on their ability to distinguish various vegetation covers. A 3 × 3 high pass filter was applied to the colour composite to further enhance visual interpretation of linear features, such as vegetation features. Supervised classification, using
Table 3: Confusion matrix validation of land-cover map 2011.

| Reference data   | Woodland | Grassland | Farmland | Sum | Producer's accuracy |
|------------------|----------|-----------|----------|-----|--------------------|
| Woodland         | 28       | 0         | 2        | 30  | 93.3               |
| Grassland        | 0        | 32        | 4        | 36  | 88.9               |
| Farmland         | 2        | 3         | 26       | 31  | 83.9               |
| Sum              | 30       | 35        | 32       | 97  |                    |
| User's accuracy  | 93.3     | 91.4      |          |     |                    |
| Overall accuracy |          |           |          |     | 88.7               |

Figure 2: Flowchart shows methodology adopted for LULC mapping by Mondal et al. [71].

2.3.2. Ground Truth. Land-cover types classified for 2011 were validated with field measurements. A hand held Global Positioning System (GPS) was used to map locations of various features and sampled land-cover observations. Using the collected ground-truth data, a final classification was done using supervised Maximum Likelihood Classifier (MLC) into three classes of interest (woodland, grassland, and cropland) (Table 1). Each observation plot was given a number and its land cover was recorded on the survey form together with the coordinate location. The development of vegetation classes was based on their clear differences in terms of physiognomy observed during the ground truthing and verification. A total of 254 ground-truth points were collected in June 2012 to serve as training samples for the classification; these points were taken in and near Serengeti (Figure 1). Training samples (number of locations and number of pixels) were distributed evenly across classes, where 70% of the data points were used for training, that is, for classification, and 30% were used for validation purposes (Table 3).

2.3.3. Classification Accuracy Assessment. The accuracy of thematic map was determined by the constructed matrices in order to test whether any difference exists in the interpretation work. The results of the image classification are validated by creating an error (confusion) matrix from which different accuracy measures are derived [46]. The confusion matrix is used to compare spatially coincident ground control points and pixels of the classified image. Table 3 shows a confusion matrix that was established using 86 ground control points (GCP) which were not used in the classification of the 2011 image. The overall accuracy, user's accuracy, and producer's accuracy were estimated from the confusion matrix. The overall accuracy, which is the number of correctly classified pixels, was divided by the total number of GCP (i.e., reference data) used for validation. The overall accuracy in the present study is 88.7% (Table 3).

2.4. Statistical Analyses. AM hyphal abundance associated with land-cover history was compared in three different land uses: wildlife-grazed system, livestock-grazed system, and cultivated soils in and near Serengeti National Park using analysis of covariance (ANCOVA). This approach tests whether or not AM hyphal abundance differed among sites that differed in their original land cover in 1984 compared to different land-use/cover transitions after controlling for relationships between AM hyphal response and three different covariates (soils P, N, and pH) found to be most important in a previous study. Candidate covariates were previously identified from among a much larger set of potential soil and...
climate variables in previous work at the same study site as shown in Soke et al. [41]. Pairwise comparisons of treatment means associated with different land use/cover changes were made by using Fisher’s Protected Least Significant Difference (LSD) at $p < 0.05$ confidence level. All statistical analyses were performed using SPSS 17.0 (IBM Corp., Chicago, US).

3. Results

3.1. Land-Use/Cover Changes in and near the Park. Generally, the maps (Figures 3 and 4) show the variation in land coverage between the two periods (1984–2011) under consideration. There were visually evident changes in land cover in and near Serengeti; outside the park, areas covered by woodlands have declined while land covers under grasslands and cultivation have expanded. Less visually apparent were frequent transitions from grassland to woodland and vice versa in uncultivated lands both inside and outside the park. A transition matrix (Table 4) summarizes the different land-cover conversions detected at the 112 sampling sites.

3.2. Influence of Land-Cover History on Soil Properties. There was no significant influence of land-cover history on soil P ($F_{1,20} = 3.17, p = 0.09$), soil pH ($F_{1,20} = 0.11, p = 0.74$), or soil N ($F_{1,20} = 0.42, p = 0.52$), among the different transitions to croplands or to grassland or to woodland in livestock-grazed sites ($F_{2,20} = 2.56, p = 0.10$). However, there was a significant influence of land-cover history on soil pH among the different transitions in livestock-grazed soils ($F_{3,44} = 2.29, p = 0.04$). There was a significant influence of land-cover history on soil P in wildlife-grazed soils ($F_{3,43} = 3.05, p = 0.04$) but not on soil N or pH ($F_{3,43} = 2.06, p = 0.12$).

3.3. Linking Land-Use Legacies and AM Hyphal Abundance. There were significant negative correlations between AM hyphal abundance and P ($r = -0.29, p = 0.02$) and N ($r = -0.25, p = 0.02$). No significant correlation was observed between AM hyphal abundance and pH ($r = 0.08, p = 0.38$). After controlling for the overall influence of soil properties on AMF abundance, there was no significant association of land-cover history with AM hyphal abundance among the different
transitions in croplands (Figure 4) \(F_{2,20} = 2.56, p = 0.13\). Within different land uses there was no significant correlation of soil P, soil N, or soil pH on AM hyphal abundance among different transitions in croplands \(F_{1,20} = 3.17, p = 0.09\). Land-cover history in livestock-grazed areas was significantly associated with AMF abundance \(F_{3,44} = 4.56, p = 0.008\) (Figure 5). Post hoc LSD multiple comparisons revealed higher AM hyphal abundance at sites that persisted as grasslands since 1984 as compared to sites that changed from woodland to grassland \((p = 0.02)\). Also, sites that changed from grasslands to woodlands had significantly lower AMF abundance in livestock-grazed system compared to sites that persisted as woodlands since 1984 \((p = 0.05)\). The unchanged woodlands had the highest abundance of AMF \((34.61 \pm 4.25 \text{ m/cm}^3)\) while sites that changed from woodlands to grasslands had the least abundance of AMF \((34.61 \pm 4.25 \text{ m/cm}^3)\). There were significant main effects of land-cover history on AM hyphal abundance among the different transitions in livestock-grazed soils after controlling for soils properties \(F_{3,37} = 3.37, p = 0.04\). There was no significant main effects of soil P, soil N, or soil pH on AM hyphal abundance among different transitions in livestock-grazed soils \(F_{1,37} = 0.75, p = 0.39\).

After controlling for the influence of soil properties, there were significant differences in AM hyphal abundance associated with land-cover history among the different transitions in wildlife-grazed soils \(F_{3,43} = 4.41, p = 0.009\). Post hoc LSD multiple comparisons revealed significantly greater AM hyphal abundance between sites that have persisted as grasslands compared to woodlands that transitioned to grasslands. There were significant main effects of land-cover history on AM hyphal abundance among the different transitions in wildlife-grazed soils \(F_{3,36} = 3.81, p = 0.02\). There were no significant main effects of soil P, soil N, or soil pH on AM hyphal abundance among different transitions in wildlife-grazed soils \((p > 0.05, \text{in all cases})\).

4. Discussion

4.1. Land-Use/Cover Changes in and near Serengeti. The results of the spatial analysis from the supervised classification of the images (Figures 3 and 4) indicate noticeable losses and gains in various land-use and land-cover types. From the classified images, it is apparent that the area covered by woodland was reduced drastically between 1984 and 2011, with an increase in grasslands and croplands (Figures 3 and 4). Natural vegetation around Serengeti ecosystem has been fragmented by human disturbances through clearance for agricultural activities and pasture [47].

The results of this study suggest that different land-cover transitions, that is, legacy effects, had relatively weak impact on AMF abundance. Only transitions from woodland to grassland in both wildlife-grazed and livestock-grazed systems were associated with 15% lower AMF abundance than that found in persistent grasslands (Figure 5). Notably, sites with transitions from grassland to woodland contained similar AMF abundance as sites that were persistent woodlands, and sites that were converted from either grassland or woodland to cropland (Figure 6) contained similar AMF abundance to persistent croplands.
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Land-cover history

0
10
20
30
40
50
60
70

AM hyphal density (m/cm³)

AG-AG G-AG W-AG

Figure 6: Mean (±SE) arbuscular mycorrhizal abundance in soils associated with various land-cover history in agricultural sites (AG: agriculture; G: grassland; W: woodland). Means with the same letter are not significantly different from each other (p < 0.05).

4.2. Association between Land-Cover History and Soil Properties. The lack of influence of land-cover transitions on AMF abundance may reflect the general lack of association in this Serengeti system between woodland and grassland and key soil properties. A history of woodland resulted in a small depression of pH that might explain the small reduction in AMF abundance associated with woodland-grassland transitions compared to persistent grasslands in livestock-grazed sites, but the change in pH is much lower than what is observed in other woodland to grassland transitions subject to use by humans [33, 47–49]. One reason for minor shifts in soil properties was that most woodlands in the Serengeti were more closed canopy savannas, with C₄ grasses in the understory similar to open grasslands. To the extent that grass understory supports AMF and maintains elevated pH through the pumping of cations from deep root layers and the recycling of cations in litter, the loss of trees in Serengeti woodlands might have only minor shifts. In protected areas subject to wildlife grazing, there was an increase in soil P at sites shifting from woodland to grassland as compared to persistent grasslands.

4.3. Association between Land-Use Legacies and AM Hyphal Abundance. However, the overall weak, land-cover history had more influence on AM hyphal abundance in livestock-grazed soils than was the case with either wildlife-grazed or cropland soils. The pattern is similar to the one reported by Aguilar-Fernández et al. [50] who found that forest sites had significantly higher AMF abundance than was the case with livestock-grazed pastures. Several studies conducted some years after forest conversion to pastures have documented a decrease in soil organic matter, microbial biomass, soil microbial activity, and nutrient losses associated with the loss of plant cover [51, 52]. However, in Serengeti, grasslands appear to contain greater AMF abundance than woodlands, perhaps because of greater belowground C inputs. Also the disruption of soil aggregates and of the processes maintaining long-term soil nutrient and water availabilities contributes to soil deterioration [53]. This study suggests that site-specific differences in soil properties may play a greater role in AM hyphal abundance as observed elsewhere [54–56].

There were significant differences in AM hyphal abundance associated with land-cover history among the different transitions in wildlife-grazed soils. Also there was a significant main effect of land-cover history on AM hyphal abundance among the different transitions in wildlife-grazed soils after controlling for soils properties. This study found that wildlife-grazed grasslands supported the highest AM hyphal abundance possibly due to the presence of more host plant biomass, suggesting that AM hyphal abundance may increase with an increase of host plant biomass and diversity. Woodlands generate a light limited environment under the canopy, which contributed to less ground plant cover (less host plants) leading to grass species suppression. This is in agreement with Burrows and Pfleger [57] who observed an increase in AMF abundance with an increase in plant species diversity. Johnson et al. [58] hypothesize that host plant species may be important for the diversity of AMF species communities.

In this study, many of the transitions may have occurred a few years prior to 2011, and some transitions may have occurred a decade or two earlier. Legacy effects of land-use changes in ecosystem functioning and services may last several hundred years [6, 7]. Different past land-cover types have long-term impacts on soil conditions and AMF abundance [6] as observed in this study.

4.4. Effects of Fire on Land Cover. Fire is recognized as a natural and important ecological factor of grassland ecosystems [59]. Fire affects nutrient cycling [60–62], modifies plant species composition [59, 63, 64], and may have legacy effects on the AMF abundance. Woodland to grassland transitions observed in this study were likely caused by fire in the park and settlement outside the park. Park managers within the Serengeti ecosystem use fire as a valuable tool to maintain the balance between grasslands and woodlands that create the iconic landscapes of the savanna [65, 66]. The constant presence of fire in the ecosystem has resulted in the evolution of fire-resistant communities of plants that are dependent on periodic burning for their existence [67]. Sometimes wildfires originate from settlement outside the park; its frequency and intensity may have effects on the biotic and abiotic components of grassland and savanna ecosystems [66, 68]. There are accounts of fire effects on ectomycorrhizal density and soil microfungi (e.g., [69]). Gibson and Hulbert [63] reported that the impact of fire has a profound effect on the vegetation. By altering soil temperatures, soil water potential, and plant species composition, burning may have both indirect and direct effects on AM fungal species composition [70].

5. Conclusions

It can be concluded that a relatively weak association between land-cover history and soil properties (pH, P, and N) among the different transitions in and near Serengeti National Park...
was observed. Furthermore, results from this study suggest that there were no relationships between AMF abundance and soil properties (pH, P, and N), regardless of the previous land-use history. AMF abundance in croplands was not significantly associated with land-cover history. For livestock-grazed areas, current grasslands that were converted from woodland since 1984 showed lower AMF abundance than areas maintained as grasslands. This suggests that overgrazing by livestock causes the reduction in AM hyphal abundance in the soils by decreasing carbon inputs. Overall, the data suggest that while current land use has a strong association with AMF abundance, land-use history has apparently little effect on AMF abundance although it might have a much stronger influence on species composition than the overall AM hyphal abundance.

Low AMF abundance in livestock areas may reflect a decrease in total carbon inputs and disturbance rather than the legacy of past land use. The degree of current disturbance (tillage and fertilizer) for croplands and reduced carbon inputs from overgrazing might make AMF abundance more vulnerable to legacy effects. A deeper understanding of various past-land-use legacies is crucial, because of their vulnerability to legacy effects. A deeper understanding of inputs from overgrazing might make AMF abundance more sensitive to disturbance rather than legacy of past land use. The degree of current disturbance (tillage and fertilizer) for croplands and reduced carbon inputs from overgrazing might make AMF abundance more vulnerable to legacy effects. A deeper understanding of various past-land-use legacies is crucial, because of their vulnerability to legacy effects.

Conflicts of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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