Land use legacy effects on woody vegetation in agricultural landscapes of south-western Ethiopia

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Abstract
Aim: Past land use legacy effects—extinction debts and immigration credits—might be particularly pronounced in regions characterized by complex and dynamic landscape change. The aim of this study was to evaluate how current woody plant species distribution, composition and richness related to historical and present land uses.

Location: A smallholder farming landscape in south-western Ethiopia.

Methods: We surveyed woody plants in 72 randomly selected 1-ha sites in farmland and grouped them into forest specialist, generalist and pioneer species. First, we investigated woody plant composition and distribution using non-metric multidimensional scaling. Second, we modelled species richness in response to historical and current distance from the forest edge. Third, we examined diameter class distributions of trees in recently converted vs. permanent farmland.

Results: Historical distance was a primary driver of woody plant composition and distribution. Generalist and pioneer species richness increased with historical distance. Forest specialists, however, did not respond to historical distance. Only few old individuals of forest specialist species remained in both recently converted and permanent farmlands.

Main conclusions: Our findings suggest that any possible extinction debt for forest specialist species in farmland at the landscape scale was rapidly paid off, possibly because farmers cleared large remnant trees. In contrast, we found substantial evidence of immigration credits in farmland for generalist and pioneer species. This suggests that long-established farmland may have unrecognized conservation values, although apparently not for forest specialist species. We suggest that conservation policies in south-western Ethiopia should recognize not only forests, but also the complementary value of the agricultural mosaic—similar to the case of European cultural landscapes. A possible future priority could be to better reintegrate forest species in the farmland mosaic.

KEYWORDS
agricultural mosaic, biodiversity conservation, extinction debt, immigration credit, novel ecosystems, nurse tree effect
Remnant woody plants in agroecosystems provide habitat and movement pathways for plants, birds, reptiles and many other species (Dorrestein, Hartel, Hanspach, von Wehrden, & Fischer, 2013; Mendenhall, Shields-Estrada, Krishnaswami, & Daily, 2016; Perfecto & Vandermeer, 2008). However, the expansion and intensification of cropland and pastures have transformed a large proportion of the planet’s land surface and are a key driver of biodiversity loss (Flinn & Marks, 2007; MA, 2005; Wright, 2010), causing habitat loss, fragmentation and persistent ecosystem changes (Foster et al., 2003; Mortelliti, Fagiani, Battisti, Capizzi, & Boitani, 2010).

While some species respond to landscape changes immediately, others exhibit a time-delayed response (Lindborg & Eriksson, 2004). Such time-delayed responses can result in two contrasting legacy effects, namely (1) an extinction debt—where the current community contains species whose populations cannot be sustained in the long term (Kuussaari et al., 2009; Tilman, May, Lehman, & Nowak, 1994), vs. (2) an immigration credit—where the environment is suitable for colonization by some species, which will gradually immigrate (Jackson & Sax, 2010). Understanding such legacy effects is crucial for devising appropriate conservation strategies. Yet, relatively few studies have investigated legacy effects of historical land use on present-day biodiversity (but see Culbert et al., 2017; Lindborg & Eriksson, 2004; Metzger et al., 2009). Of the notable exceptions, most have focused on aggregate patterns of species richness and composition (e.g., Häger, Fernández Otárola, Stuhlmacher, Acuña Castillo, & Contreras Arias, 2015; McNeely & Schroth, 2006; Tolera, Asfaw, Lemenih, & Karlton, 2008), paying relatively little attention to differences between species of different conservation status or habitat affinity. When disaggregating species, however, it is possible that the same system experiences extinction debts and immigration credits in different locations. For example, an agricultural frontier landscape may temporarily retain relict forest species in recently cleared farmland (an extinction debt), but may gradually accumulate new communities of generalist and pioneer species in longer-established farmland (an immigration credit; Figure 1).

Both extinction debt and immigration credit are influenced by multiple factors including species life history traits (e.g., longevity, dispersal capacity), history of landscape composition and habitat configuration, the extent of habitat change and stochastic processes (Hylander & Ehrén, 2013; Jackson & Sax, 2010; Kuussaari et al., 2009). For example, some long-lived forest trees species can persist for more than a century after forest fragmentation (Vellend et al., 2006). In contrast, short-lived butterfly species showed no remaining extinction debt 40 years after habitat change (Krauss et al., 2010). Likewise, the establishment and survival of a species in a new location are contingent on its dispersal mechanisms and interactions with the existing community (Davis, Grime, & Thompson, 2000; Essl et al., 2015; Sakai et al., 2001). Time-delayed responses can also depend on the extent of habitat change in size, quality and connectivity (Hylander & Ehrén, 2013; Jackson & Sax, 2010; Pardini, de Bueno, Gardiner, Prado, & Metzger, 2010). Typically, extinction debts and immigration credits are less likely to exist in landscapes with little and isolated habitat, after severe disturbance (Hanski & Ovaskainen, 2002; Helm, Hanski, & Pärtel, 2006; Tilman et al., 1994).

In this study, we evaluated legacy effects in an agricultural region in south-western Ethiopia. Here, crop-based subsistence agriculture began in the mid-19th century (McCann, 1995) and since the 1970s has become a major driver of land use change (Kassa, Dondeyne, Poesen, Frankl, & Nyssen, 2016). Currently, agricultural policies encourage cereal crop production by distributing improved seeds and chemical fertilizers, which may induce further deforestation and land degradation (Hylander, Nemomissa, Delrue, & Enkosa, 2013; Kassa et al., 2016). Because of the high rate of deforestation and high concentration of endemic plant and bird species, the region is considered part of the Eastern Afromontane Biodiversity Hotspot (Reusing, 2000; Schmitt, 2006). Despite ongoing land use change, the region is still dominated by smallholder farming and still comprises a mosaic of forest patches, home gardens and pastures.

**FIGURE 1** Conceptual framework figure of the historical landscape, and its complex and dynamic change in response to various management practices. For example, tree retention and planting can lead to an extinction debt—persistence of forest specialist species, while establishment and survival of new generalist and pioneer species within the farmland can lead to an immigration credit.
The landscape matrix is rich in trees (Figure 2) (e.g., Jara, Hylander, & Nemomissa, 2017), which are used for many purposes—for example as shade for coffee, live fences, honey production or for domestic wood products (Ango, Börjeson, Senbeta, & Hylander, 2014). Trees in the landscape matrix can be assumed to fulfill important ecosystem functions (Manning, Fischer, & Lindenmayer, 2006) and contribute substantially to local biodiversity (Engelen, Lemessa, Şekercioğlu, & Hylander, 2016; Gove, Hylander, Nemomisa, & Shimelis, 2008; Hylander & Nemomissa, 2008).

Considering ongoing complex and dynamic landscape changes in south-western Ethiopia, it is plausible that species diversity and composition could be affected by legacy effects. Such effects can be expected to be particularly pronounced for long-lived woody species. To account for legacy effects and develop appropriate conservation strategies, we therefore sought to understand the possible presence of both extinction debts and immigration credits in the region. Focusing on woody species within the farmed sections of the landscapes (i.e., outside large tracts of forest), we reasoned that both an extinction debt and an immigration credit could be inferred when present-day species diversity was better described by past rather than present-day landscape characteristics (Hanski, 2000; Kuussaari et al., 2009; Lindborg & Eriksson, 2004). An extinction debt following habitat loss and fragmentation was assumed to occur when locations that were historically within the forest had retained high forest species richness, while locations historically within farmland had few species. In a system that is characterized by gradual loss of forest cover (Hylander et al., 2013), locations that were historically far from the forest edge (i.e., deep within farmland; point D in Figure 1) can be assumed to have been converted earlier than locations closer to the historical forest edge (point C in Figure 1), while locations forested at the historical reference time were converted even later (points B and A in Figure 1, respectively). For instance, in another agricultural landscape in southern Ethiopia, the richness of forest specialist epiphytic plants decreased with distance to forest (Hylander & Nemomissa, 2017). In contrast, an immigration credit was assumed to occur in the opposite case—when locations that were historically far from the forest (and are still far from forest) have more species than locations that were historically close to the forest. Such a situation would imply that farmland, once established, gains species through time (Figure 1) (Hanski, 2000; Jackson & Sax, 2010; Lira, Ewers, Banks-Leite, Pardini, & Metzger, 2012), because of gradual increases in structural complexity and the gradual, natural addition of non-forest species to the community. For example, native Oromo people in Ethiopia may choose to retain and protect fig trees (Ficus spp.), practice home garden agroforestry, use trees for traditional coffee management (Getahun, 2016; Jara, Hylander, & Nemomissa, 2017) and, in many locations in farmland, simply allow for natural regeneration processes of “useful” species to take place.
Using this framing, we hypothesized the following:

1. Present-day land use variables, especially current distance from the forest edge, influence woody plant species richness, composition and distribution.

2. Legacy effects of historical land use influence woody plant community composition, distribution and species richness, with possible extinction debts for forest specialist species, and possible immigration credits for species that can regenerate in farmland environments.

3. Legacy effects may also be detectable from site-level population structures—for example, large diameter forest specialist trees may have largely disappeared in long-established farmland but may still persist in recently converted farmland.

2 | METHODS

2.1 | Study area

The study was conducted in the rural landscapes of six kebeles (the smallest administrative unit in Ethiopia), located in Gera, Gumay and Setema districts of Jimma Zone, Oromia Regional State, southwestern Ethiopia (Figure 3). The study kebeles comprised a mosaic of land use types, with forest cover ranging from 11 to 84 percentage, while arable land, grazing land and settlements accounted for the rest. In the study area, coffee is an economically important cash crop. It is grown at different levels of intensity, mostly in patches of remnant forest, and occurs primarily between 1,550 and 1,900 m altitude.

2.2 | Site selection

Within each kebele, we determined the proportion of arable land and grazing land (hereafter, jointly referred to as “farmland”) using a land cover map generated via supervised image classification of a RapidEye satellite image from 2015. We randomly selected 72 circular 1-ha survey sites across the six kebeles—53 in arable land and 19 in grazing land, assigned proportionally to the occurrence of arable land and grazing land in each kebele. Here, although the centre of these sites was always located in arable land or grazing land, in some instances the edge of the sites also comprised other land uses, such as life fences, home gardens or small plantings or remnant patches of trees.

2.3 | Woody plant surveys

We surveyed woody plants from 01 November 2015 to 30 January 2016 in all 72 sites. We recorded all individuals of tree and shrub to subshrub species with height ≥1.5 m, and also measured and recorded diameter at breast height (DBH) of all individuals with DBH ≥5 cm. As the occurrence of young trees is typically correlated with the presence of seedlings (recent regeneration) in a given site (e.g., Fischer et al., 2009), for logistical reasons, we chose not to count individuals <1.5 m in height for this study. We identified plants that were readily identifiable in the field. For species that were difficult to identify in the field, specimens were collected, pressed, dried and transported to the National Herbarium at Addis Ababa University for identification. Very few specimens of relatively rare species could not be identified to species level and were identified to genus level, or in one case treated as an “unidentified” species. Species were further groupings as forest specialist, generalist and pioneer based on relevant literature (Flora of Ethiopia and Eritrea, 1989–2006; Hundera et al., 2013; Teketay, 1997; Tesfaye, Teketay, & Fetene, 2002; see Table S1). Nomenclature follows the Flora of Ethiopia and Eritrea (1989–2006).

2.4 | Land use characteristics and environmental parameters

We distinguished between current distance vs. historical distance from the forest edge to obtain proxies for current landscape position and historical landscape position of farmland sites relative to a gradually reclining forest edge (Hylander et al., 2013; Lindborg & Eriksson, 2004). Current distance was derived from the RapidEye land cover classification (Figure 3d). All current distances were positive, denoting the distance from the centre of the survey site to the nearest current forest patch of at least 1 ha in area (Figure 1). Historical forest cover was derived from a supervised image classification of a Landsat image from 1973 (Landsat 1-MSS, obtained from http://www.usgs.gov/) using ArcGIS 10.2 (Figure 3c). We calculated the historical distance of our current study sites from the nearest historical forest edge, again considering only forest patches of at least 1 ha in area. Notably, historical distances to the forest edge were positive when the current farmland site was historically farmland (points C and D in Figure 1) and negative when the current farmland site was historically forested (points A and B in Figure 1). This way, we distinguished between "permanent" farmland sites (those historically also farmland) vs. "converted" farmland sites (those historically forested; Table 1). Notably, for this study, all sampling sites were selected within current farmland (i.e., excluding the few instances where farmland had changed into forest; see Table 1).

We also considered other key environmental variables that we believed might affect woody plant richness and composition as covariates, namely site-level forest cover (i.e., the current proportion of woody vegetation cover within the 1-ha circular site as a measure of available wooded habitat); a terrain wetness index; altitude; and the type of site (grazing vs. arable site). The ASTER Digital Elevation Model (obtained from https://reverb.echo.nasa.gov/) was used to derive altitude and the wetness index (following Fischer et al. (2010)). All variables were calculated in ArcMap 10.2. These variables were not of primary interest but were included because they may account for additional variability in the data. An overview of the variables and their description are provided in Table 2.
2.5 | Statistical analysis

The analysis followed three steps. First, we investigated patterns in community composition. Second, we modelled total richness of all plant species combined (i.e., pooled), as well as richness of forest specialist, generalist and pioneer species in response to the explanatory variables (Table 2). Third, we examined site-level population structure of all trees of forest specialist, generalist and pioneer species in converted and permanent farmland by comparing DBH size class frequency distributions.

2.5.1 | Species composition analysis

Using the presence–absence data of species in all study sites, we conducted non-metric multidimensional scaling (NMDS, with Bray–Curtis distance measure) to visualize general patterns of species
composition. We tested whether the study site scores correlated with historical distance, current distance, site forest cover, land use type, wetness index, altitude and converted vs. permanent farm-land status, using the “envfit” function in the “vegan” package in R (Oksanen et al., 2017).

2.5.2 | Species richness models

We used generalized linear mixed effects models (GLMMs) with a Poisson error structure to investigate the effects of current distance, historical distance, site forest cover, land use type (arable vs. grazing), wetness index and altitude on richness of (1) all woody species, (2) forest specialist species, (3) generalist species and (4) pioneer species. Our primary interest in these models was in the effects of current and historical distance, while other variables were included primarily to filter out unwanted variability. In all cases, we specified kebele (to account for grouping in experimental units) and an observation-level dummy variable (to account for overdispersion) as random effects (Table 2). Prior to modelling, we checked for possible correlations among explanatory variables—all correlations were below 0.4. Furthermore, we log-transformed current distance and site forest cover to remove skew, and scaled all continuous variables to zero mean and unit variance to obtain standardized coefficients. We assessed the models using “DHARMa,” an R package for residual diagnostics of GLMMs that uses a simulation-based approach (Hartig, 2016). Finally, to visualize effects, we predicted species richness values and their 95% confidence intervals in response to historical distance and current distance to the forest edge.

2.5.3 | DBH size class distribution

As a proxy for site-level population structure, we investigated DBH size class distribution of (1) forest specialist tree species, (2) generalist

<table>
<thead>
<tr>
<th>Type</th>
<th>Variable</th>
<th>Definition and method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed effect</td>
<td>Current distance</td>
<td>The distance in m of the centre of the site from nearest current (2015) forest edge (Figure 3d)</td>
</tr>
<tr>
<td>Historical distance</td>
<td>The distance in m of the centre of the site from nearest historical (1973) forest edge (Figure 3c)</td>
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<tr>
<td>Altitude</td>
<td>Altitude above sea level derived from the ASTER DEM</td>
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<tr>
<td>Site forest cover</td>
<td>Proportion of woody vegetation cover within 1-ha study site calculated from classified RapidEye image (2015)</td>
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<tr>
<td>Wetness index</td>
<td>Measure of potential soil wetness, estimated by the topographic position in the landscape and the slope (after Fischer et al., 2010)</td>
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<td>Land use type</td>
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<td>Random effect</td>
<td>Kebele</td>
<td>Smallest administrative unit within which sites were nested</td>
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<tr>
<td>Dummy</td>
<td>Observation-level random effect to account for overdispersion</td>
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<tr>
<th>Type</th>
<th>Variable</th>
<th>Definition and method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites with current (2015) distance &lt;100 m</td>
<td>Sites with current (2015) distance &gt;100 m</td>
<td>Sites with historical (1973) distance &gt;100 m</td>
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<tr>
<td>Sites with current (2015) distance &lt;100 m</td>
<td>Sites with current (2015) distance &gt;100 m</td>
<td>Sites with historical (1973) distance &gt;100 m</td>
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<td>9</td>
<td>16</td>
<td>25</td>
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**TABLE 1** Overview of the surveyed 1-ha sites in terms of their current and historical landscape position relative to forest patches of at least 1 ha in size

**TABLE 2** Definition and description of the explanatory variables used to model plant species richness
tree species and (3) pioneer tree species, using data pooled across sites. We compared the mean number of individuals per hectare across diameter classes in converted vs. permanent farmland sites.

3 | RESULTS

3.1 | Overview and species composition

A total of 110 (one unidentified) species of trees, shrubs and sub-shrubs representing 48 families were recorded from all study sites (Table S1). Non-metric multidimensional scaling (NMDS, two-dimensional ordination; stress = 0.237) showed distinct locations occupied by forest specialist species when compared to generalist and pioneer species (Figure 4a). Historical distance to forest was positively correlated with generalist and pioneer species, clustering in the more distant farmland sites (Figure 4b). Forest specialist species were positively associated with higher altitudes (Figure 4b).

3.2 | Species richness models

Richness of generalist and pioneer species—but not forest specialist species—increased with historical distance from the forest edge (Table 3; Figure 5c,e). A lower richness of generalists was found in grazing land than in arable land (Table 3).

As expected, richness of all species groups was positively related to the amount of forest cover available at a site (Table 3). Richness of all species combined and pioneer species declined with topographic wetness, and altitude was negatively related to all species combined, generalist and pioneer species richness (Table 3).

3.3 | DBH size class distribution

The site-level population structure of different species of forest specialists—but not generalist and pioneer species—differed between recently converted vs. permanent farmland (Figure 6a–f). In converted farmland, trees of forest specialist species were represented with many individuals in the lowest DBH classes and a few individuals in the highest class (Figure 6a). Permanent farmland also had many young individuals, but hosted slightly fewer large individuals (Figure 6b). Generalist and pioneer species generally were represented with a relatively large number of small individuals followed by a gradual decrease in individuals towards higher size classes—with diameters following an inverted J-shaped distribution in both converted and permanent farmlands (Figure 6c–f).

4 | DISCUSSION

Delayed effects pose a major challenge to conservation because they can be easily overlooked (Hylander & Ehrlén, 2013; Jackson & Sax, 2010; Kuussaari et al., 2009). Focusing on a biodiverse region characterized by dynamic changes in forest and farmland cover, we found evidence of past land use legacy effects, with statistically significant effects of historical land cover variables on richness of generalist and pioneer species.
We found only partial confirmation of our first hypothesis that present-day land use structures—including grazing land vs. arable land, and current distance from the forest edge—influenced woody plant species richness, composition and distribution. Only generalist species richness was affected by farmland type. In contrast, our second hypothesis—that legacy effects of historical land use would influence woody plant species—was largely confirmed. We identified significant relationships between historical distance and richness of generalist and pioneer species. However, unexpectedly, no association was found between forest specialist species richness and historical distance from the forest edge. The dominant legacy effect identified through this second hypothesis thus was that of an immigration credit, rather than extinction debt.

Our third hypothesis—that diameter size distributions would show legacy effects—had only weak support. As compared to permanent farmland, recently converted farmland had slightly more large relict forest trees, which may be interpreted as a site-level extinction debt. In contrast, the site-level population structure for trees of other groups of species was close to what might be expected for natural populations in both converted and permanent farmland sites. In the following, we discuss these findings in relation to the concepts of extinction debt vs. immigration credit, and we try to explain what may have led to these delayed effects of land cover change.

Regarding extinction debts, we found only weak support for forest specialist species (see above). This suggests that whatever extinction debt exists for forest species appears to be rapidly “paid off” after conversion of forest to farmland. A possible driver may be farmers’ management practices. Farmers in the same landscapes were previously found to have removed big trees selectively to create open fields and reduce damage of crop raiding wild mammals, which may use big trees for shelter (Ango et al., 2014). Similarly, farmers may also be discouraged from retaining big forest species on their farmland by conservation policies that prohibit using the wood of many native species (Lemenih & Kassa, 2014). The few remaining

<table>
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<th>Coefficient</th>
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<th>p-Value</th>
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<td>0.068</td>
<td>&lt;.001 ***</td>
</tr>
<tr>
<td></td>
<td>Historical distance</td>
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<td>0.060</td>
<td>.292</td>
</tr>
<tr>
<td></td>
<td>Current distance</td>
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<td>0.064</td>
<td>.746</td>
</tr>
<tr>
<td></td>
<td>Site forest cover</td>
<td>0.314</td>
<td>0.063</td>
<td>&lt;.001 ***</td>
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<tr>
<td></td>
<td>Wetness index</td>
<td>−0.155</td>
<td>0.062</td>
<td>.013 *</td>
</tr>
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<td></td>
<td>Altitude</td>
<td>−0.192</td>
<td>0.065</td>
<td>.003 **</td>
</tr>
<tr>
<td></td>
<td>Land use type</td>
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<td>0.121</td>
<td>.386</td>
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| Forest specialist species richness | Intercept | 0.843 | 0.168 | <.001 *** |
|                                   | Historical distance | −0.153 | 0.153 | .316 |
|                                   | Current distance      | 0.029    | 0.100 | .769 |
|                                   | Site forest cover      | 0.391    | 0.106 | <.001 *** |
|                                   | Wetness index          | −0.014   | 0.098 | .890 |
|                                   | Altitude               | 0.238    | 0.149 | .110 |
|                                   | Land use type          | 0.071    | 0.209 | .734 |

| Pioneer species richness       | Intercept | 1.649 | 0.087 | <.001 *** |
|                               | Historical distance | 0.149    | 0.073 | .041 * |
|                               | Current distance     | −0.034   | 0.081 | .674 |
|                               | Site forest cover     | 0.239    | 0.077 | .002 ** |
|                               | Wetness index         | −0.232   | 0.080 | .004 ** |
|                               | Altitude              | −0.334   | 0.082 | <.001 *** |
|                               | Land use type         | −0.008   | 0.164 | .961 |

| Generalist species richness    | Intercept | 1.517 | 0.065 | <.001 *** |
|                               | Historical distance | 0.132    | 0.059 | .026 * |
|                               | Current distance     | 0.038    | 0.063 | .541 |
|                               | Site forest cover     | 0.332    | 0.057 | <.001 *** |
|                               | Wetness index         | −0.107   | 0.062 | .085 |
|                               | Altitude              | −0.236   | 0.065 | <.001 *** |
|                               | Land use type         | −0.276   | 0.137 | .043 * |

Predictor terms are continuous except for land use type. Coefficient for land use type indicates the difference between grazing and arable land, with arable land being the reference level. Significance levels are indicated by: *p < .05; **p < .01; ***p < .001.
older forest trees that we recorded in farmland can therefore be expected to soon disappear.

Surprisingly, we found substantial evidence of immigration credits in farmland. Immigration credits were identified for generalist and pioneer species richness. We interpret this finding in relation to three ideas—possible nurse tree effects in increasingly old farmland, the development of a novel ecosystem and, subsequently, the gradual evolution of a cultural landscape.

A nurse tree effect describes the process by which an existing tree facilitates the establishment, survival and growth of colonizers through improved microclimatic conditions, increased water and nutrient availability, protection against herbivory, provision of shelter for seed-dispersing birds and mammals and sometimes attraction of pollinators (Bruno, Stachowicz, & Bertness, 2003; Feyera, Beck, & Lüttge, 2002; Padilla & Pugnaire, 2006). For example, in Ethiopia plantations of exotic trees had a nurse effect for the establishment and growth of various native plants (Feyera et al., 2002; Teilla, Hylander, & Nemomissa, 2015). Similarly, invasion of weed plants was facilitated by a native nitrogen-fixing shrub in California coastal prairie (Maron & Connors, 1996). Nurse tree effects might also be assisted by deliberate (e.g., in some Oromo landscapes people preserve and protect Ficus trees; Getahun, 2016) or inadvertent human actions, because the colonizing species involved often have associations with human disturbance (Sax & Brown, 2000). Through time, human actions combined with a small number of trees planted or retained in farmland thus could provide a nurse tree function to other species—resulting in an accumulation of species through time, and thus explaining the positive effect on species richness of increasingly isolated old farmland sites.

Possibly facilitated by nurse tree processes, changes in tree communities with historical distance could thus signal the development of ‘novel ecosystems’ (Hobbs, Higgs, & Harris, 2009; Hobbs et al., 2006; Milton, 2003). Novel ecosystems are characterized by new combinations of species, often including a mixture of native, introduced and planted species. For example, land use change has resulted in novel bird species assemblages in Australia (Lindenmayer et al., 2008), new associations of native and non-native perennial plants in tropical agroforestry systems (Ewel, 1999), including in

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**FIGURE 5** Effects of historical and current land use on the species richness of total species (panels (a) and (b)), pioneer species (panels (c) and (d)) and generalist species (panels (e) and (f)). Solid lines indicate model predictions for arable land while other variables were held constant at their means; dashed lines indicate 95% confidence intervals. The x-axes display original values but all distances are scaled and current distances are on a logarithmic scale.
south-western Ethiopia (Hylander & Nemomissa, 2017; Jara et al., 2017). Moreover, novel ecosystems are characterized by altered potential ecosystem functions and human agency—that is, they result from deliberate or unintentional human action (Hobbs et al., 2006). Novel ecosystems may be considered as threats to the structures, coherence and identity of existing landscapes (Antrop, 2005), but also as opportunities for their potential to deliver new sets of benefits, both ecologically and socially—as shown, for example, for a novel forest ecosystem on Ascension Island (Wilkinson, 2004). Concerns about novel ecosystems should be viewed in terms of their sustainability, and questions of its relative value in terms of the ecosystem functions and services provided or lost (Hobbs et al., 2006). For instance, nutrient cycling rates do not necessarily depend on particular species in a particular location, and hence, substitution of one species by another may have limited impact—resulting, in this context, in no measurable consequence for ecosystem functioning (Ewel & Putz, 2004). By contrast, the location of particular species in particular places should, by definition, be a key consideration of what to conserve or restore and where, and thus remains a key focus of conservation policies (Hobbs et al., 2009).

Assuming that species-rich farmland (especially adjacent to traditional coffee farming practices; e.g., Gove et al., 2008; Hylander & Nemomissa, 2008; Jara et al., 2017) is more desirable than species-poor farmland, one may also consider that the observed immigration credit of trees in farmland signals the gradual emergence of a unique, species-rich cultural landscape. Cultural landscapes are places where people have interacted with and shaped nature over long periods of time (Plieninger, Höchtl, & Spek, 2006). They are characterized by a stable and distinct identity, a system of sustainable land uses, and their biodiversity typically mirrors a complex history of compositional and structural change (Antrop, 2005; Farina, 2000; Phillips, 1998). Recognizing this, biodiversity conservation in cultural landscapes is an important conservation paradigm in the developed world, particularly in Europe, and especially after devastating landscape changes following

**FIGURE 6** Diameter at breast height (DBH) size class distribution of individuals/ha of (a) and (b) trees of forest specialist species; (c) and (d) generalist species; and (e) and (f) pioneer species in converted and permanent land use, respectively. The y-axes display original densities on a logarithmic scale. DBH classes are 1 < 5 cm; 2 = 5.1–10 cm; 3 = 10.1–20 cm; 4 = 20.1–30 cm; 5 = 30.1–40 cm; 6 = 40.1–50 cm; 7 = 50.1–60 cm; 8 = 60.1–70 cm and 9 > 70 cm.
the industrial revolution (Déjeant-Pons, 2006; Vos & Meekes, 1999; Wright, Lake, & Dolman, 2012). In Europe, the appreciation of cultural landscapes is based on society’s demand for multifunctionality, interest and engagement of farmers, support from national and local authorities, and, finally, decentralization of landscape ruling and legislation, which favours regional solutions (Vos & Meekes, 1999). Against this backdrop, our results serve as a potential warning sign for obvious changes already taking place in Ethiopia and suggest an urgent need for new approaches to biodiversity conservation across entire landscape mosaics. Key properties underpinning the biodiversity values of cultural landscapes include a diversity of land covers and their spatial heterogeneity (Dorresteijn, Loos, Hanspach, & Fischer, 2015). To the best of our knowledge, the idea of thinking about agricultural landscapes as cultural landscapes is poorly established in Africa, but our findings suggest this idea deserves further consideration.

4.1 | Conservation implications

Through the use of satellite imagery and field data, we revealed biodiversity effects of current and historical land use for landscapes in south-western Ethiopia. Our study showed distinct legacy effects, most notably an immigration credit in farmland for generalist and pioneer species richness and composition. Such legacy effects can lead to novel species combinations and novel ecosystems, which may be seen as a threat to the structure, coherence and identity of existing systems; or as an opportunity for the development of sustainable cultural landscapes. To safeguard valuable biodiversity in agricultural landscapes of south-western Ethiopia and other similar parts of the globe, we suggest to: (1) broaden the focus of conservation policies to encompass the entire landscape mosaic including both forest and farmland; (2) manage agricultural landscapes as a cultural landscape, actively fostering species diversity; (3) consider possible benefits of maintaining forest specialist species in the farmland mosaic, both for human use and biodiversity conservation; and (4) harness research opportunities that existing yet rapidly disappearing traditional farming systems provide to understand social-ecological dynamics.

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DATA ACCESSIBILITY

All data used for the analysis are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1kd43s5.

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SUPPORTING INFORMATION

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