Drivers of species richness and community integrity of small forest patches in an agricultural landscape

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**Abstract**

**Questions:** Long-term fragmentation and land use in Europe have created a landscape pattern where small forest patches are embedded among agricultural landscapes. These small forest patches can be one of the few habitats left to maintain the species richness and ecosystem functions within intensively managed agroecosystems. We ask, which factors determine vascular plant species richness, community composition and forest community integrity in small forest patches in an agricultural landscape?

**Location:** NE Estonia.

**Methods:** We combine island biogeographic theory (patch area and isolation) with the properties of the surrounding landscape and local environmental conditions within a patch to study the drivers of species richness and community integrity.

**Results:** Patch area together with local environmental factors (understorey light conditions and soil reaction) determined both species richness and community integrity. Total species richness and forest generalists were related to patch area alone, whereas forest specialists were additionally dependent on patch light conditions. Species richness of grassland specialists in the forest patches increased with the amount of natural habitat in the surrounding landscape, while the presence of synanthropic species was positively related to soil reaction. Forest community integrity was higher in larger, more shaded patches with low soil reaction, which together defined suitable conditions for forest communities and hindered the intrusion of species from other habitats.

**Conclusions:** Under a suitable set of conditions, encompassing both favourable landscape and local environmental conditions, even small forest patches can provide habitat for both forest and grassland communities in agricultural landscapes. Comprehensive approaches, considering species composition, environment and landscape conditions simultaneously, are needed for making reliable predictions of biodiversity patterns.
1 | INTRODUCTION

Small forest patches (forest fragments with area up to 50 ha) are a common feature in European agricultural landscapes (Decoècq et al., 2016; Schmithüsen & Hirsch, 2010). Active land use has increased forest fragmentation in Europe over many centuries (Eriksson, Skånes, Hammer, & Lönn, 2010; Vellend et al., 2006), resulting in strongly fragmented landscapes where a large proportion of patches are very small, only up to a couple of hectares in size (Estreguil, Caudullo, de Rigo, & San Miguel, 2012; Schmithüsen & Hirsch, 2010). Most forest patches are relatively recently formed secondary patches on former woodland or agricultural areas (Decoècq et al., 2016; Grashof-Bokdam, 1997; Harmer, Peterken, Kerr, & Poulton, 2001). Some patches, however, have remained relatively untouched in places unsuitable for agriculture and forestry due to remoteness, topographic or edaphic reasons (Graae, Økland, Petersen, Jensen, & Fritzøeørga ø, 2004; Jacquemyn, Butaye, & Hermy, 2001; Laurance, 2008). Despite their small size, small forest patches can provide a number of ecosystem services, such as regulation of pests (Bianchi, Goedhart, & Baveco, 2008; Mitchell, Bennett, & Gonzalez, 2014), nutrient and water cycling (Mitchell et al., 2014; Weathers, Cadenasso, & Pickett, 2001) and provide a valuable habitat for many organism groups (Decoècq et al., 2016; Honnay, Hermy, & Coppin, 1999).

Biodiversity in fragmented habitat patches is often explained according to the principles of the island biogeographic theory (MacArthur & Wilson, 1963, 1967) and metacommunity theory (Leibold et al., 2004) by emphasizing the effect of patch area and isolation. In forest patches, the importance of both area and isolation for plant species richness has indeed been recorded in numerous studies (Jacquemyn et al., 2001; Liira et al., 2008; De Sanctis, Alfò, Attorre, Francesconi, & Bruno, 2010; Humphrey et al., 2015). In addition, the habitat amount hypothesis was suggested more recently by Fahrig (2013), proposing that habitat amount within a landscape is more important than focal patch area and isolation. The amount of forest in the landscape has, indeed, also been found to be important for tree species richness, abundance and regeneration in forest patches (Benchimol et al., 2017; Rocha-Santos et al., 2017). However, for a more comprehensive understanding of the processes affecting biodiversity in fragmented habitat systems, these theories need to be expanded to take into account other important factors affecting species richness (Haila, 2002; Laurance, 2008), such as local patch environment (Dupré & Ehrlén, 2002; Hodgson, Mollanen, Wintle, & Thomas, 2011; Kolb & Diekmann, 2004), patch heterogeneity (Honnay et al., 1999; Valdés et al., 2015; Wulf & Kolk, 2014), management regime (Lawesson et al., 1998; Liira, Jürjendal, & Paal, 2014) and landscape matrix (Buffa, Del Vecchio, Fantinato, & Milano, 2018; Kupfer, Malanson, & Franklin, 2006; Paal, Kütt, Löhmus, & Liira, 2017).

For a better understanding of what influences species in forest patches, it is important to follow species groups with different ecological preferences in addition to total species richness (Buffa et al., 2018; Kolb & Diekmann, 2005; Paal et al., 2017; Rodríguez-Loinaz, Amezaga, & Onaindia, 2012). Species with different preferences, for instance habitat specialists vs. generalists or characteristic vs. derived species (sensu Helm, Zobel, Moles, Szava-Kovats, & Pärtel, 2015), form heterogeneous species pools that have distinct responses to particular landscape and environmental factors (Helm et al., 2015; Jamoneau et al., 2011; Paal et al., 2017). For example, unlike other groups, forest specialists in particular are most often found related to patch isolation (Deckers, De Becker, Honnay, Hermy, & Muys, 2005; Graae, 2000; Jamoneau et al., 2011; Rodríguez-Loinaz et al., 2012), but also to patch size (Guirado, Pino, & Rodà, 2006; Kolb & Diekmann, 2004) and quality (Dupré & Ehrlén, 2002; Hérault & Honnay, 2005; Wulf & Kolk, 2014).

Forest generalist species (species that also grow in forest edges, clearings, grasslands and are more disturbance-tolerant), on the contrary, are generally less affected by patch isolation than forest specialists (Kolb & Diekmann, 2004; Paal et al., 2017; Rodríguez-Loinaz et al., 2012). However, a larger amount of forest in the surrounding landscape can still favour their richness (Paal et al., 2017). High-quality forest patch interior is not as essential for forest generalists, compared to forest specialists (Rodríguez-Loinaz et al., 2012), but environmental conditions, such as soil moisture, nutrients and topography, can still have an effect on their richness (Kolb & Diekmann, 2004; Wulf & Kolk, 2014).

Additional species in forests, such as grassland specialists and synanthropic species (plants mainly found in anthropogenic habitats), are affected by an altogether different set of factors. Grassland specialists, growing at forest edges and gaps, are considerably less affected by fragmentation than forest species (Lindborg et al., 2012), but are negatively related to the intensity of agriculture around the patch (Jamoneau et al., 2011). At the same time, synanthropic species are positively related to the intensity of human disturbances (Guirado, Pino, & Rodà, 2007), intensity of agriculture in the matrix (Liira et al., 2008) and negatively connected to patch size (Guirado et al., 2006). Poor light conditions in forests can also hinder the infiltration of non-forest plants (Bossuyt, Hermy, & Deckers, 1999; Honnay, Jacquemyn, Bossuyt, & Hermy, 2005; Liira, Löhmus, & Tuisk, 2012), whereas improved light conditions under intensive management can promote their growth (Sepp & Liira, 2009).

Plant communities in fragmented and anthropogenic landscapes, therefore, consist of species groups with different historical
backgrounds, habitat preferences and human tolerance rates, forming heterogeneous and often shifted species pools (Guirado et al., 2007; Helm et al., 2015; Liira et al., 2008). Human impact through habitat fragmentation, direct disturbance and the intrusion of synanthropic and other non-characteristic species can reduce community integrity—the condition of a community and its ability to support the composition and functions characteristic to it—and make communities more vulnerable to further perturbations (Helm et al., 2015; Larsson, 2001; Noss, 1983; Tierney, Faber-Langendoen, Mitchell, Shriver, & Gibbs, 2009). To help to predict biodiversity differences and possible future changes in communities and landscapes, it is useful to distinguish species groups with different ecological preferences and responses to the surrounding conditions (e.g., forest specialists, grassland specialist, synanthropic species). Examining the relationships of these species groups within a community enables us to understand the sensitivity of different species groups and community integrity to various environmental and stress factors (Guirado et al., 2007; Noss, 1990; Paal et al., 2017; Rodríguez-Loinaz et al., 2012). This in turn directs us to a better understanding of how to manage these communities and maintain the important elements of the ecosystem without damaging human use of the landscape.

In this study, we examine small forest islands amid an agricultural landscape—we estimate their importance as refugia for biodiversity in intensively used landscapes and test the factors influencing their

**FIGURE 1** Hypothetical expected connections between the landscape and local factors (centre) influencing species richness (left) and community integrity indices (right) in small forest patches

**FIGURE 2** Studied forest patches within agricultural landscape in northeast Estonia. Most of the uncultivated areas in the region are affected by karst formations. Note that patch 24, which used to be the largest patch, was mostly clear-cut shortly before the survey, with only the southwestern edge of the forest remaining. Map: Estonian Land Board (xgis.maaamet.ee)
plant species richness and community integrity. We combine patch configuration (area and isolation) from the island biogeography theory, with the composition of the surrounding landscape and local patch environmental conditions to reveal the factors determining vascular plant species richness. We use community composition and community integrity indices to evaluate the conservation value of forest patches and study the factors influencing it. Our specific hypotheses are presented in Figure 1.

2 | METHODS

2.1 | Study area

We surveyed 27 small forest patches in an agricultural landscape in Estonia (59°16’N, 26°13’E), Northeast Europe, located within an area about 20 km² (Figure 2). Bedrock in this region is Ordovician limestone, covered with rendzic leptosols and gleysols (Estonian Land Board, xgis.maaamet.ee). Karst formations are frequent in the area. Average temperature in February is −4.8°C and in July 17.1°C, annual precipitation is about 600 mm (Estonian Weather Service; www.ilmateenistus.ee).

All studied patches have uneven topography compared to the surrounding agricultural areas. Most patches are located on karst formations and are often lower (by 1–2 m) than the surrounding landscape, others are on positive land forms slightly higher (by 1–2 m) than the surroundings (Supporting information Appendix S1). Variable topography has probably prevented intensive management of these patches and, most likely, they have never been ploughed. Due to the small area of most patches, their exact area on older maps (e.g., the end of 19th century one-verst map of the Russian Empire; 1:42,000) cannot be determined, but their size has probably varied over time. The aerial photographs from 1952 show that several patches were not covered by forest and were most likely used as pastures or grazed woodland at the time (Archived orthophotos from 1952, Estonian Land Board). Nevertheless, all patches were afforested by the beginning of the 1980s (Külvik, 1984). Visible traces on site indicate that some woodcutting, including partial clearcutting, has occurred at different times in about half of the patches. Currently, meadows and different arable fields, with main crops of grains and legumes, surround the patches.

2.2 | Vegetation sampling

Vegetation sampling was carried out in June and July of 2015 and 2016. In 2015, transect sampling was carried out in each forest patch (more details in Supporting information Appendix S2). To assemble complete species pools (list of all vascular plants) for each forest patch, we also noted all the species outside the transects. In 2016 we revisited all sampled forest patches to complete the species pools. We inspected thoroughly each forest patch and the buffer zone of herbaceous vegetation separating the forest from crop fields, which spans 1–3 m from the forest edge.

2.3 | Environmental data

The mean amount of light in each forest patch was calculated based on the analysis of fisheye photos (hemispherical photography technique; Anderson, 1964). The photos were taken during two clear and sunny days in August 2015. A single photo was taken above the herb layer of each quadrat at about 50-cm height. The measurements were averaged for the whole patch. From the photos, the total PPFD (photosynthetic photon flux density; mol m⁻² day⁻¹) was calculated with WinSCANOPY 2005a (Regent Instruments, Quebec, CA). Soil samples were taken in August and September 2015 from the centre of at least three quadrats per transect and the results were averaged for the whole forest patch. Soil reaction (in 0.01 M KCl solution with soil to solution ratio of 1:2.5), nitrogen content (%), Dumas dry combustion method) and humus layer depth (cm) were measured. Patch moisture conditions (mesic or temporarily wet) were recorded on site by visual inspection.

2.4 | Landscape data

Estonian Land Board 1:10,000 orthophotos from 2013 were used to map the current outer border of the forest patches. The landscape parameters (patch area, isolation and surrounding landscape composition) were calculated based on the Estonian Basic Map data (Estonian Land Board, 2016). To characterize patch isolation, distance to the nearest forest patch (considering all patches in the landscape, not only our focal patches), to the nearest patch at least 1 ha and at least 10 ha in size were calculated. The composition of the surrounding landscape was determined within four buffer zones, with a radius of 100, 200, 500 and 1,000 m from the edge of each forest patch. The amount of forest sensu latu (including forest and shrubland), and anthropogenic areas (including cultivated land, buildings and roads) in the surrounding landscape were determined and used in subsequent analyses. For digitizing and calculations, GIS program MapInfo Professional 12.5 was used (Pitney Bowes Software, Stamford, CT, USA, 2014).

2.5 | Species habitat preferences and community integrity indices

We divided all species (both woody and herbaceous) in four categories based on their habitat preference in the Estonian flora key (Leht, 2010). Each species was checked for the habitats listed in the key and divided into one of four categories: (a) forest specialists—species that grow only in forest habitats; (b) forest generalists – species that grow in forests, grasslands, forest edges and clearings; (c) grassland specialists – species that grow only in grassland habitats; (d) synanthropic species – species that are mainly found in different anthropogenic habitats (such as road verges, fields, waste lands) and cultivated species.

Community integrity, an aspect of a wider concept of ecological integrity, is used to describe the capacity of a system to support and preserve the characteristic composition and functions of
the community similar to the unimpaired natural community (De Leo & Levin, 1997; Noss, 1990; Tierney et al., 2009). To examine forest community integrity in our forest patches and study the factors that influence it, we used the index of Favourable Conservation Status (FCS; ln(characteristic diversity/derived diversity)), that can be used as a measure of biodiversity integrity and community condition (Helm et al., 2015; Kasari, Saar, de Bello, Takkis, & Helm, 2016). In our study, we use the FCS, for the first time in forest communities (to our best knowledge). We use three related indices to outline different processes affecting forest community integrity. (a) FCS,—the log ratio of forest specialists to derived diversity (Helm et al., 2015).

We define characteristic species as only forest specialist species (for an alternative approach and results see Supporting information Appendix S3). As derived species (those not typical for the habitat, and whose diversity is often driven by the negative human impact; Helm et al., 2015), we use all other species in the community. Furthermore, to investigate more specifically the invasion by species from other native communities (Valéry, Fritz, Lefeuvre, & Simberloff, 2009), we excluded forest generalists and calculated (b) the log ratio of forest specialists to species from non-forest communities (grassland specialists and synanthropic species). Finally, to outline more specifically the changes in community integrity related to human activities that have allowed the invasion of synanthropic species, we calculated (c) the log ratio of forest specialists to synanthropic species.

2.6 | Data analysis

All statistical analyses were conducted in R 3.4.2 (R Foundation for Statistical Computing, Vienna, Austria). Positive-only data were log-transformed, and composition of surrounding landscape and soil N content data were logit transformed to overcome the restrictions of percentage data. Explanatory variables were tested for multicollinearity using variance inflation factors (VIF) and the function ‘vif’ in the package ‘car’ (Fox & Weisberg, 2011). Because of strong collinearity with other parameters (VIF > 3), the composition of the surrounding landscape within a 200-m radius was excluded from further analysis. The effect of selective cutting in forest patches (cut over or under 25% of patch area) was evaluated with the Fischer’s exact test. The effect was non-significant for most test variables and confounded with the effect of patch area, therefore woodcutting was not taken into account in the following models. Several patch shape indices were also calculated, but due to a strong correlation between patch area and the best indices, the indices were not included in the models (for more information see Supporting information Appendix S4).

We grouped the explanatory variables in four groups: (a) isolation parameters (distance to the closest forest patch, distance to the closest 1 ha forest patch and distance to the closest 10 ha forest patch); (b) local environmental conditions in the patch (soil reaction, soil N content, humus layer depth and total amount of light); and two groups of surrounding landscape parameters—(c) the amount of forest in the surrounding landscape (within 100, 500 and 1,000) and (d) the amount of anthropogenic land in the surrounding landscape (within 100, 500 and 1,000 m). The two components of the surrounding landscape were relatively strongly correlated with each other within each buffer zone (VIF > 3), therefore their effect was modelled separately.

We tested the effect of these parameters on the total species richness, richness of all habitat specialist groups (forest specialists, forest generalists, grassland specialists and synanthropic species; all including both herbaceous and woody species) and the three integrity indices. We also tested separately the effect of all parameters on the number of trees and woody species, except for the amount of light, which directly depends on tree and shrub cover.

As a first step, we built linear models within the four groups to find the most important factors in each group. We used AIC-based model averaging on the best models (delta < 7; Burnham & Anderson, 2002), calculated with the R function ‘mod.avg’ in package ‘MuMIn’. As a result, averaged Akaike weights (\(\hat{\theta}\) ) are calculated for each tested parameter, indicating their relative importance across all averaged models (Burnham & Anderson, 2002). Confidence intervals (95%, calculated based on the best models with the function ‘confint’ in the same package) were used to evaluate parameter significance, and only those deemed significant were used in the second step.

As a second step, the significant parameters from the first models were combined to find the most important drivers over all relevant factors. Forest patch area, as a core factor, was added to each model. Separate models were built with the two components of the surrounding landscape to avoid collinearity. The same AIC-based model averaging approach was used as in the first step.

3 | RESULTS

The studied forest patches were mostly very small, only 0.02–11.38 ha (median 0.18 ha, average 0.85 ha). The numerous patches in this area are relatively close to each other – the distance to the closest patch was 3–224 m (median 20 m, average 51 m). The total number of species per patch varied between 73 and 152 (average 94). Even the smallest patches had some forest specialists (2–18 species per patch), even though the number of forest generalists (28–71 species), grassland specialists (14–50 species) and synanthropic species (4–34 species) at each patch was generally higher (Supporting information Appendix S1).

Linear models showed that the total species richness, richness of trees and all woody species, and forest generalist richness were positively dependent on patch area alone, whereas forest specialists are related to both patch area (positively) and the amount of light (negatively; Figure 3, Tables 1, 2). The number of grassland specialists was negatively related to the amount of anthropogenic land within 1,000 m radius, while the number of synanthropic species was dependent on soil acidity, with more species on neutral soils (around pH 6.8–7.2) and less species on slightly acidic soils (around pH 6.3–6.5). The number of trees and all woody species per patch was positively related to patch area (Table 1). Forest integrity indices were associated with patch area and local environmental conditions
(amount of light and soil reaction), similar to species richness measures (Figure 3, Table 1).

4 | DISCUSSION

Species diversity and community integrity in small forest patches depended on a combination of factors, including both patch configuration and local environmental conditions. Total species richness, as well as the number of trees and all woody plants, was determined significantly only by patch area, thus partially supporting the application of the island biogeography models in such systems. A positive species-area relationship, as suggested by the island biogeography theory, is often found for forest patches (Buffa et al., 2018; De Sanctis et al., 2010; Decocq et al., 2016; Dumortier et al., 2002), particularly for older patches (>51 years; Jacquemyn et al., 2001; Liira et al., 2008) and those with a small area, like most of our patches (<5 ha; Wulf & Kolk, 2014). Surprisingly, patch isolation and composition of the surrounding landscape, despite being significant in numerous earlier

TABLE 1 Importance of predictors (averaged Akaike weights; $\hat{\theta}$) in determining species richness and community integrity in the second step of linear models

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Patch area (ha)</th>
<th>Distance (m) to the closest</th>
<th>Amount of light (mol m$^{-2}$ d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>forest patch</td>
<td>1 ha forest</td>
</tr>
<tr>
<td>Total species richness</td>
<td>27</td>
<td>0.82 (4/+</td>
<td>0.55 (4/−)</td>
<td>1.00 (2/−)</td>
</tr>
<tr>
<td>Forest specialists</td>
<td>27</td>
<td>1.00 (2/+</td>
<td>1.00 (2/+</td>
<td>1.00 (2/+</td>
</tr>
<tr>
<td>Forest generalists</td>
<td>27</td>
<td>1.00 (2/+</td>
<td>1.00 (2/+</td>
<td>1.00 (2/+</td>
</tr>
<tr>
<td>Grassland specialists</td>
<td>27</td>
<td>0.28 (2/−)</td>
<td>0.34 (2/+</td>
<td>0.32 (2/−)</td>
</tr>
<tr>
<td>Synanthropic species</td>
<td>26</td>
<td>0.34 (2/+</td>
<td>0.81 (2/+</td>
<td>0.76 (4/+</td>
</tr>
<tr>
<td>Forest specialists/all other species</td>
<td>27</td>
<td>0.61 (8/−)</td>
<td>0.61 (8/−)</td>
<td>0.85 (8/−)</td>
</tr>
</tbody>
</table>

Notes. In parentheses are the number of models in which the predictor was present and the effect (positive or negative). Numbers in bold indicate significant parameters (based on 95% confidence intervals). The amount of forest and anthropogenic land were modelled separately to avoid collinearity, therefore there are two models presented for some dependent variables.

$^a$Mesic or temporarily wet soils.
studies (Kupfer et al., 2006; Jamoneau et al., 2011; Fahrig, 2013; Humphrey et al., 2015), had little or no effect on species richness in our system. Their low impact could be explained by a relatively high connectivity of patches (Butaye, Jacquemyn, & Hermy, 2001; Grashof-Bokdam, 1997; Jacquemyn, Butaye, & Hermy, 2003a). Although no effect of the local environmental conditions was found on total species richness, the effect was more apparent when analysing species groups separately and when testing community integrity indices.

4.1 Patterns of species groups

Forest-associated taxa, both forest specialists and generalists, were strongly dependent on patch area. However, in addition to area, forest specialist richness was also related to patch light conditions. Patch area is often considered important for determining forest specialist richness because of a relatively larger patch interior area with more suitable conditions, such as appropriate shading, for specialist species (Kolb & Diekmann, 2004; Rodriguez-Loinaz et al., 2012). Nevertheless, even the smallest patches harboured at least some forest specialists, possibly because of the high connectivity of forest patches in the studied system, which could allow for seed dispersal despite the generally low dispersal ability of forest specialists (Brudvig, Mabry, & Mottl, 2011; Honnay et al., 2005; Jacquemyn et al., 2001). At the same time, forest generalist species in our system were positively dependent on patch area alone. Their lack of association with environmental factors can be related to their wider ecological tolerance (Kolb & Diekmann, 2005; Paal et al., 2017; Rodriguez-Loinaz et al., 2012).

Grassland specialist richness was negatively related to the amount of anthropogenic land in a 1000-m radius. In patches with more anthropogenic land in the surroundings, there is less natural vegetation that can help maintain grassland plant populations and retain their species richness (Evju, Blumentrath, Skarpaas, Stabbettorp, & Sverdrup-Thygeson, 2015; Humphrey et al., 2015; Krauss, Klein, Steffan-Dewenter, & Tscharntke, 2004). Grassland species are generally considered better dispersers than forest specialists, although they too cannot cope with extensive isolation (Lindborg et al., 2012; Lindborg, Plue, Andersson, & Cousins, 2014; Soons, Messelink, Jongejans, & Heil, 2005). The dependence of grassland specialist richness on the surrounding landscape within the largest tested buffer zone (1,000-m radius) confirms the wide connection network of grassland species in this landscape. Surprisingly, the richness of grassland species was not directly connected to patch light conditions, contrary to expectations (Bossuyt et al., 1999; Honnay et al., 2005; Honnay, Verheyen, & Hermy, 2002). This could be explained by the fact that most common grassland herbaceous species in Estonia have been shown to benefit from partial shading (Semchenko, Lepik, Götzenberger, & Zobel, 2012). It is also possible that these small forest patches contain enough areas with sufficient light within the patches, or at least in the shape of the narrow natural grassland band around the woodland, to support the persistence of grassland specialists and to enable maintenance of their meta-populations in the agricultural landscape (Lindborg et al., 2014).

### TABLE 1

<table>
<thead>
<tr>
<th>Soil reaction</th>
<th>Soil N (%)</th>
<th>Humus layer (cm)</th>
<th>Soil humiditya</th>
<th>Amount of forest within (m)</th>
<th>Amount of anthropogenic landscape within (m)</th>
</tr>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100</td>
<td>500</td>
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<tr>
<td>Soil reaction</td>
<td></td>
<td></td>
<td></td>
<td>0.33 (4/-)</td>
<td>0.19 (1/-)</td>
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<tr>
<td>1.00 (4/+))</td>
<td></td>
<td></td>
<td></td>
<td>0.87 (2/-)</td>
<td>0.24 (2/+))</td>
</tr>
<tr>
<td>0.70 (4/-)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>1.00 (13/-)</td>
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<td></td>
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<tr>
<td>1.00 (11/-)</td>
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</table>
The only significant relationship of synanthropic species richness was found for soil reaction, with slightly acidic soils harbouring less synanthropic species than patches with neutral soil. Soil reaction is very important for determining plant ecological range and vegetation variations in forest patches (Diekmann, 1994; Dumortier et al., 2002; Dupré & Ehrén, 2002; Hérault & Honnay, 2005; Jacquemyn, Butaye, & Hermy, 2003b). Soil reaction becomes moderately more acidic during forest development and is generally lower than soil reaction in agricultural lands and meadows (Harmer et al., 2001; Verheyen & Hermy, 2001; Snakin, Prisyazhnaya, & Kovács-Láng, 2001). Possibly, species related to human activities prefer more neutral or basic soils (which also prevail in the study region) and avoid forest patches with slightly acidic conditions. Surprisingly, there was no effect of the amount of anthropogenic land in the surroundings on the synanthropic species (Guirado et al., 2007; Liira et al., 2008). This could be explained by the fact that the region in northeast Estonia, where our study system is located, is traditionally one of the most intensely cultivated areas in the country (Peterson & Aunap, 1998), where synanthropic species have probably been present for a long time, with the local dispersal supported by a dense road network, numerous cattle, etc.

### 4.2 Patterns of community integrity

Our analyses show that, similar to grasslands (Helm et al., 2015; Kasari et al., 2016), the integrity indices (FSC, and related indices) provide a useful tool for estimating community condition also in forest systems and for studying the factors influencing community integrity. Forest integrity at our patches was determined by the synergy of patch configuration and environmental conditions. Community integrity was higher in larger patches, similar to the richness of forest specialist and generalist species. However, the configuration of a patch also needs to be supported by suitable environmental conditions to maintain high community integrity (Valdés et al., 2015).

Environmental conditions can either aid or hinder the infiltration of non-characteristic species into the community, and thus have an important role in supporting communities with high integrity. In our system, light availability was one of the main predictors related to all three tested integrity indices. Forest specialist species are more shade-tolerant, even compared to forest generalists (Harmer et al., 2001; Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999; Paal et al., 2017). Therefore, lower light availability defines the favourable conditions for forest specialists and supports their prevalence over other species (Bossuyt et al., 1999; Harmer et al., 2001; Liira et al., 2012; Paal et al., 2017).

Soil reaction affected community integrity by limiting the invasion of non-forest species—grassland and synanthropic species—to forest communities. Soil reaction appears particularly important for preventing the infiltration of synanthropic species, considering also its direct effect on synanthropic species richness. A similar limiting effect of soil reaction has also been found in Belgian forests for the intrusion of weedy plants into the forest interior, coupled with the
effect of low light conditions (Honay et al., 2002). Altogether, larger patches with slightly acidic soil and low light appear to be most resistant to the invasion of synanthropic and other non-forest species and can be regarded as a ‘stronghold’ for higher integrity forest communities among these small forest patches.

We conclude that small forest patches in generally impoverished agricultural landscapes can harbour diverse communities and help provide ecosystem services. A suitable set of conditions, which include both favourable patch configuration (mainly larger patch areas) and environmental conditions (low light and slightly acidic soil reaction), support forest community integrity even in relatively small patches. In addition to offering habitat for forest communities, small forest patches can also act as refugia for grassland specialists and thus promote the overall biodiversity in agricultural landscapes. Moreover, different species groups within patch species pools had distinctly different responses to landscape structure and environmental conditions. This suggests that applying a relatively simple theoretical framework, like the island biogeography model, i.e. without accounting for patch environment and the surrounding landscape, and analysing the total richness as a whole, might not provide reliable predictions for actual biodiversity patterns. We need to expand our approach and use more comprehensive models in order to estimate more accurately both current patterns and potential changes in these patterns due to land-use and climate change.

AUTHOR CONTRIBUTIONS

TiK and MK conceived the idea and designed the study; TiK, TH, PJ, KKal, KKau, ThK, OK, KL, ML, IM, HP, JR, KsA, KSe, ÜV and LL collected the data; KT analysed the data; KT and LL led the writing of the manuscript. All authors contributed to the manuscript and approved it for publication.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Site properties of the studied forest patches

**Appendix S2.** Vegetation sampling transects

**Appendix S3.** Alternative community integrity indices and models

**Appendix S4.** Patch shape indices

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