TITLE

The European Turtle Dove in the ecotone between woodland and farmland: multi-scale habitat associations and implications for the design of management interventions

RUNNING TITLE

Turtle Dove habitat associations review

AUTHORS

Carles Carboneras[1,2]*, Lara Moreno-Zarate[1], Beatriz Arroyo[1]

AUTHORS' AFFILIATIONS

1 – Instituto de Investigación en Recursos Cinegéticos (IREC) (CSIC-UCLM-JCCM), Ciudad Real, Spain

2 – RSPB Centre for Conservation Science, Sandy, United Kingdom

* – corresponding author: carles.carboneras@rspb.org.uk

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Abstract

The European Turtle Dove (turtle dove) is a globally threatened species that is undergoing a sustained and generalised decline across its breeding range, with habitat deterioration and loss suggested as the main driver. Here, we review the scientific literature on habitat associations across the European breeding range, in relation to turtle dove distribution, breeding numbers, nesting substrates and food and foraging habitats, to identify optimal habitat management measures. Large-scale (national) distribution seemed to depend on the availability, but not dominance, of forest; abundance at the landscape scale was generally higher in woodland than on farmland, highlighting the importance of forest habitats for the species. However, abundance in woodland increased with additional structural diversity and proximity to farmland, and abundance on farmland increased with greater availability of non-farmland features (including forest patches, shrubs, hedges), indicating a preference in this species for a mixture of habitats. Nesting occurred most frequently on trees (secondarily on bushes) but we found geographical differences in the type of nesting substrate, with thorny bushes (or trees with lianas) being used more frequently in the north, and open canopy trees (including ever-green oaks and olive trees) in the south. Turtle doves used a wide spectrum of food items with a predominance of wild seeds, particularly of early-flowering plants, but we could not identify a single plant species whose abundance determined turtle dove numbers. In several parts of the distribution range, a shift from wild to cultivated seeds occurred as the season progressed. However, various results indicate that interventions to improve food availability should favour the provision of wild seeds rather than of crop seeds. Our review indicates that the most efficient habitat management interventions depend on the dominant landscape (farmland or woodland) and that, overall, interventions should seek to augment the heterogeneity of the landscape by increasing the mixing of farmland and woodland. Forestry and agricultural policies should be combined to provide the right conditions for species that favour the ecotone between woodland and farmland, like the turtle dove.

Keywords: *Streptopelia turtur*, European Turtle-dove, migratory species, migrant, conservation, vulnerable, threatened, Species Action Plan

INTRODUCTION

The globally threatened European Turtle Dove (*Streptopelia turtur*; hereafter, turtle dove) is one of Europe's most rapidly declining species and a priority for conservation. In 2015, it was uplisted to the IUCN Vulnerable category, following a >30% population loss in 3 generations (BirdLife International 2015). The first EU management plan on the species (Boutin & Lutz 2007) failed to achieve its conservation objectives. Following that, an International Single Species Action Plan (SAP) (Fisher *et al.* 2018) was adopted to tackle the main identified threats: habitat loss and deterioration on the breeding and wintering grounds, illegal killing and unsustainable hunting during migration. The top conservation objective of the turtle dove SAP was to maintain and increase good quality habitats on the breeding grounds, with available and accessible water and food. Recognising further that current knowledge may be biased towards a small part of its distribution, an additional objective of the turtle dove SAP was to improve knowledge of habitat selection and dietary needs on the breeding grounds across its wide range. An improved understanding of the relationships between habitat and occurrence, numbers and nesting preferences would allow designing better management.

Although frequently portrayed as a farmland specialist (Dunn *et al.* 2018, PECBMS 2020), a wealth of published work indicates that the turtle dove occupies a wider range of habitats during the breeding season, generally at low altitude (mostly below ca. 1000 m a.s.l.) and often combining open ground (arable or grassland) with hedges, trees or small woods (Kotov 1974, Peiró 1990, Dias & Fontoura 1996, Mason & Macdonald 2000, Browne *et al.* 2004, Browne & Aebischer 2005). Dominant extensive woodland as well as heath are apparently avoided at least in some areas (Bijlsma 1985, Gutiérrez 2001) but young plantations and managed woodlands, felled or coppiced, may hold high densities of breeding turtle doves (Kraus *et al.* 1972, Bijlsma 1985, Genard 1989, Gaitzenauer 1990, Browne *et al.* 2004, Fuller *et al.* 2004). The species has also been described as favouring disturbed conditions and typically not being found in climax plant communities. Thus, at a time when the species was abundant in the UK, the ecotone where deciduous woodland gives way to open grassland was described as its preferred habitat (Murton 1968).

The European Turtle-dove occupies a very large breeding range; for comparison, it is equivalent to 32-65 times the size of France, western Europe's largest country (Newton 1995, BirdLife International 2021). In this massive area, turtle doves must necessarily associate with multiple habitats and diverse landscapes. Our aim was to determine whether habitat associations in this species are general or context-specific because this may have implications on whether recommendations for habitat management deduced from one particular area could be applicable elsewhere.

We reviewed the literature on turtle dove habitat associations across its European distribution at several spatial scales, from the breeding range (continental scale) to the individual nesting tree. We explored the relationship of habitat with large-scale distribution and of landscape characteristics with variations in density, and we examined studies of nesting and foraging habitats. As there was relatively little information on the latter, we also reviewed information on diet as a surrogate for habitats that would be suitable for foraging. We discuss our results in terms of habitat management for the species, and in terms of ecological requirements across some parts of the species' vast range.

METHODS

We started by searching all the literature referenced in the two action plans (Boutin & Lutz 2007, Fisher *et al.* 2018) and the seven PhD theses (Rocha 1999, Browne 2002, Dias 2016, Gutiérrez-Galán 2017, Marx 2018, Bermúdez 2020, Moreno Zárate 2021) known to us that focused on the turtle dove's European breeding grounds. In addition, we reviewed all the papers cited in those works as well as all the recent literature on the species, through searches on the Web of Science (apps.webofknowledge.com), Google Scholar (scholar.google.com) and Connected Papers (www.connectedpapers.com) websites using the keywords "Streptopelia turtur" and "turtle dove", alone and in combination with "habitat", "farmland", "woodland" and "diet".

We restricted our analyses to the European breeding grounds, for two reasons. One was that the European part of the distribution is occupied by a single subspecies, *turtur*, taxonomically different to the three forms breeding in North Africa and Asia (Baptista *et al.* 2020). The second reason was that our objective was not to describe the habits of the species at large but to provide a synthesis of evidence to help improve habitat management on the breeding grounds, to complement the propositions of the SAP, and we were interested in proposing habitat management measures that are applicable within this range as part of the SAP. Like it, we focussed especially on the populations of *turtur* that have suffered, or risk undergoing, the heaviest declines. We however compared our findings with information from other areas (e.g., North Africa) when appropriate.

For plant species described as being consumed by turtle doves, we assessed whether they were annual, biennial or perennial according to information in World Flora Online (www.worldfloraonline.org), Encyclopedia of Life (www.eol.org) and Flora Ibérica (www.floraiberica.es). For studies made in the Iberian Peninsula, we also assessed flowering phenology from Flora-On www.flora-on.pt. We restricted that assessment to Iberia because the onset of spring progresses markedly from SW to NE throughout Europe (Menzel *et al.* 2005) and the Portuguese dataset was the only one available with complete phenological information including the very early part of the season.

RESULTS

Turtle dove large-scale distribution

On a broad continental scale, the distribution of turtle doves appeared mostly associated to lower latitudes and warmer temperatures. The results of the distribution model for the second European Breeding Bird Atlas, EBBA2 (Keller *et al.* 2020), showed that latitude had the single heaviest weight (32.5%) in predicting the probability of occurrence (PO) and that PO decreased sharply north of the 48° N line. Several additional variables related to temperature had a combined weight of 42% (Supporting Online Information table S1). Of these, the most important climatic variables were the mean temperature during the entire breeding season, with a weight of 24%, and the mean annual temperature, with 5.5%. The European breeding distribution pattern thus fits with that of a thermophilic species linked to sustained warm temperatures over prolonged periods, confirming earlier studies at national level in Germany and the UK (Norris 1960, Kraus *et al.* 1972). Overall, >85% of PO in EBBA2 came from abiotic factors (geographic, climatic, human density, soil type), while factors associated to habitat contributed less than 15% to the model. On a continental scale, the only land cover variable with any significant effect in predicting turtle dove PO was rainfed (= non-irrigated) cropland (weight: 6%), with a positive relationship (Keller *et al.* 2020).

At a lower (national) scale, abiotic variables also seemed to be more important than land use to explain distribution in Germany (Marx & Quillfeldt 2018), mainly mild minimum temperatures in January (which might be linked to food availability during the early breeding season) and lower precipitation during the warmest quarter (which might relate to nestling survival), although models also suggested a quadratic relationship with forest cover, i.e., positive effects on PO when canopy closure was >40% but negative when it was >60%.

In contrast, habitat characteristics seemed to be a much stronger determinant of distribution in Spain than topo-climatic factors. A study on turtle dove distribution at national scale (Moreno-Zarate *et al.* 2020) showed that turtle dove occurrence was positively but quadratically related to the availability of coniferous forests, sclerophyllous vegetation, olive groves and orchards, areas of complex cultivation patterns and mosaics of farmland and natural vegetation, and the dominance of any of those vegetation types led to a decrease in PO.

Relationships between habitat and breeding numbers at the landscape scale

We found 32 studies, summarised in Tables 1a and 1b, that compared turtle dove abundance or other related variables across different habitats in European landscapes: one third from the UK, another third from Spain, and the rest from several different countries.

In most areas, abundance was generally higher in woodland than on farmland; the only exceptions came from one study in the UK and two studies in Spain (Table 1b). However, the two studies in Spain compared densities across very disjunct areas (Table 1a), so their results may be influenced by spatial variation in abundance for reasons unrelated to habitat (e.g., if the proportion of woodland is higher in study areas of higher altitude). Where assessed (one study each in Spain, Italy, Portugal and Bulgaria), riparian forests also showed high average densities compared to other habitats (Table 1a).

In forest habitats, several features were associated with high turtle dove densities (Table 1b), including increased structure diversity; open canopy and thin tree cover; forest clearings with grassy undergrowth; forest stands of intermediate age/size; and proximity to farmland.

On farmland, higher abundance in the UK, France, Italy, Austria and northern Spain was associated to the availability of hedgerows, windbreaks and woodland edges (Table 1b); in Mediterranean environments of the Iberian Peninsula, higher abundance was found in areas with high availability of tree crops. The presence of patches of natural vegetation (scrub, natural woodland, or fallow) and of water bodies also appeared to have positive effects for turtle doves on farmland.

Some of the 32 studies provided a sufficiently detailed description of the study sites, or it was possible to infer their characteristics from those of the general area, to allow a deeper understanding of the relationship between breeding numbers and habitat structure; they are summarised in Table 2. Assessment of those studies showed that in landscapes dominated by semi-natural habitats (i.e., where the unmanaged or non-farmland components within the farmland landscape occupied the biggest portion), turtle doves appeared to be more abundant in broadleaved or Mediterranean mixed woodland with an open canopy and a herbaceous understorey. Most often, grassy understoreys in those areas were associated with grazing or browsing herbivores.

In semi-transformed landscapes, where farmland mixed with unmanaged forested areas at the landscape level, the combination of trees and open spaces associated with higher breeding densities was more varied, although turtle doves also consistently associated with open canopy cover and an herbaceous understorey. Densities in broadleaved or mixed woodland were generally higher than in tree crops and conifers and, in turn, those held higher numbers than more open spaces such as arable land or grassland. Riparian forests also had high densities (although not necessarily the highest) in this type of landscape. The association with herbivory for maintaining the herbaceous understory was weaker (Table 2).

Where the farmland component of the landscape clearly dominated and wooded / unmanaged elements were small or isolated, turtle doves appeared to prefer wild or planted broadleaved and mixed stands, even if occurring in dense formations with closed canopy and a woody understorey (Table 2). More open habitats, such as residential areas, pasture and arable, had relatively lower nesting densities, and shrubs and hedgerows were commonly mentioned for breeding but not necessarily as the species' first choice.

Several of the above-mentioned studies also highlighted the positive effect of unpaved tracks on breeding densities (Mason & Macdonald 2000, Bermúdez 2020, Vreugdenhil-Rowlands 2020). This may be related to the association of tracks with ruderal plants (see also below) and the fact that seeds may be more easily accessible in the bare areas of tracks, or else to the fact that tracks increase landscape heterogeneity.

Most of the studies reviewed (Tables 1a, 1b and 2) were correlational; however, a few studies were quasi-experimental, showing before-after relationships. In Catalonia (Spain), a forest management experiment linked to wildfire prevention showed that turtle doves responded positively to undergrowth clearing; their numbers increased following the removal of the understorey and the thinning of trees (Camprodon & Brotons 2006). In Kent (UK), after the coppicing of a plot of Sweet Chestnut *Castanea silva* forest, numbers of turtle dove gradually increased and peaked when the forest was 14 years, by which time the canopy had closed, the field layer had disappeared, and the ground was bare (Fuller & Moreton 1987). A rewilding experiment in the UK saw territories increase from 0 to 16 following the restoration of intensive farmland to its natural uncultivated state and the introduction of herbivores. The rootling action of pigs was shown to favour annual ruderal plants, although the direct effect on turtle doves was not demonstrated (Tree 2018, Klee 2019). Finally, also in the UK, the deployment of agri-environment schemes aiming to provide seed-rich habitats for turtle doves resulted in a slower temporal decline in the abundance of breeding males on intervention sites, reflecting enhanced habitat suitability for territory settlement (Dunn *et al.* 2021).

Nesting substrates

We found 18 studies containing information on the relative frequency of nest substrates used on the European breeding grounds, totalling more than 1600 nests (Table 3). Nests were reported from a wide variety of trees and shrubs, revealing great flexibility in this species. We found indication of a latitudinal variation along the western flyway in the relative use of different nest substrates (Fig. 1). Nests were most commonly situated on thorny bushes in more northerly areas, and these were replaced progressively further south by broadleaved trees and conifers, later by evergreen trees (*Quercus*) and finally by olive groves in southern Iberia.

The regular presence of climbers ('lianas') on or over the nest was mentioned in some studies from France and UK (Aubineau & Boutin 1998, Browne & Aebischer 2004, Lormée 2015), and suggested as a protection to improve breeding success. In Mediterranean environments, nests were generally more exposed, often on dispersed trees, and devoid of climbers (Sáenz de Buruaga *et al.* 2013, Dias 2016, Arroyo *et al.* 2019). Further east, in Austria, nests were often situated in prickly bushes, arguably to protect them from corvid predation (Gaitzenauer 1990); in Bulgaria, nests were found predominantly on deciduous broadleaved and fruit trees (Nankinov 1994), but no mention was made of their association with thorns or lianas.

Food, and feeding habitats

The large number of seed types reported in studies from breeding grounds across Europe shows the wide variety of seeds consumed by the species (Table 4). Using the four categories in Dunn *et al.*'s (2018) analysis, most taxonomic units on the list of seed types are known to occur naturally in the environment (78%), whilst only 11% are cultivated (Table 4). Some seed types appeared to be particularly favoured, either because of their size, nutritional value or accessibility, including, e.g., species of *Amaranthaceae, Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Fabaceae, Geraniaceae, Papaveraceae, Poaceae, Polygonaceae, Primulaceae, Ranunculaceae* and *Violaceae*, as well as nettles *Urtica*. In general, the species was found to feed mainly on annual ruderal plants growing wildly in disturbed environments (Fig. 2, Table 4). However, there was not one plant species to which Turtle dove abundance or distribution would be particularly linked, and Irby's (1875) claims about the close association with *Cerinthe major* in Andalucía, Murton *et al.*'s (1964) about *Fumaria officinalis* in Britain or Gutiérrez-Galán *et al.*'s (2019) about *Echium plantagineum* also in Andalucía probably described only local phenomena, rather than general associations.

We assessed the flowering phenology for the species reportedly taken as food in the Iberian Peninsula (Dias & Fontoura 1996, Jiménez et al. 1992, Gutiérrez-Galan & Alonso 2016). This showed that most species mentioned had long flowering periods (starting in April or before, and finishing in June-July or later), with many species taken showing flowering peaks in April and June (Fig. 3).

Few studies analysed the use of foraging habitat separately from that of breeding habitat. Turtle doves were mentioned to feed invariably on the ground, with several studies describing their principal habitat requirement for feeding as weed-rich areas with low open vegetation cover, hayfields, field strips, tracks and also as an herbaceous understorey within forests or on land disturbed through tillage, burning or grazing (Mason & Macdonald 2000, Browne & Aebischer 2003a, Bakaloudis *et al.* 2009, Dias *et al.* 2013, Gutiérrez-Galán *et al.* 2019, Moreno-Zarate *et al.* 2020, Vreugdenhil-Rowlands 2020). Birds tended to feed more often in natural environments during the first half of the breeding season and there was generalised use of man-made structures (spilt grain, livestock feed, manure heaps, maintained feeding sites and harvested stubbles) during the second half (Browne 2002, Browne & Aebischer 2003a, Gutiérrez-Galán & Alonso 2016, Dunn *et al.* 2018). The use of supplementary food (grain) provided during or at the end of the breeding season has thus been suggested as an emergency conservation measure for the species (Fisher *et al.* 2018) and is regularly used as part of hunting management (https://www.fundacionartemisan.com/investigacion/ pirte). A study in Spain (Rocha & Quillfeldt 2015) showed that sites where grain had been provided had a higher young/adult ratio in the birds observed by mid-August, suggesting that local breeding success could have been enhanced. On the other hand, Dunn *et al.* (2021) did not find better breeding success or better nestling condition in areas where improved foraging habitats had been provided, and the physical condition was worse in nestlings fed with crop seeds rather than those fed with wild seeds (Dunn *et al.* 2015).

Most studies assumed that most foraging occurred within or near the breeding territories and, therefore, authors often recommended conservation interventions intended to provide seed-rich habitat in close proximity to suitable nesting habitat (Browne *et al.* 2004, Browne & Aebischer 2005, Dunn & Morris 2012, Fisher *et al.* 2018, Moreno-Zarate *et al.* 2020). While this could be true for a majority of Turtle dove territories, use of tracking technology has revealed that feeding sites could be spatially disjunct from breeding sites by up to 10 km (Calladine *et al.* 1997, Browne & Aebischer 2003a, Gutiérrez-Galán & Alonso 2016, Arroyo *et al.* 2019, Vreugdenhil-Rowlands 2020). A recent study on farmland showed that home range size decreased with an increasing proportion of non-farmed habitat in the home range (Dunn *et al.* 2021), indicating that food was likely more easily obtained in the semi-natural parts of the farmland area; however, the presence of seed-rich habitats led to larger home ranges, suggesting that turtle doves expanded their home ranges to exploit those favoured areas. In general, turtle doves were shown to use grassland for foraging more often than expected from their availability, indicating that it was a preferred foraging habitat.

DISCUSSION

The European Turtle Dove as an ecotone species

Our review has shown that the turtle dove should not be considered to associate predominantly to farmland, but rather to the ecotone between forest and farmland, as stated by Murton (1968). Overall, large-scale (e.g., national) distribution seemed to be more linked to the availability (but not dominance) of forest, and abundance at the landscape scale was also higher in woodland than on farmland. However, abundance increased in woodland when it was more structurally diverse and it was closer to farmland, and abundance on farmland increased with the presence of non-farmland features (e.g., forest patches, shrubs or hedges), highlighting the preference for a mixture of habitats in this species.

Our review also showed a large variation in nesting substrates and food types consumed by turtle doves in line with the species' broad distribution over different habitats; this shows that the species can potentially adapt to a variety of habitats as far as they provide necessary nesting and feeding resources.

We discuss these topics below.

Geographical variation in use of nesting substrates

The available studies on nest site selection differed in search methodology, and this may influence the likelihood of finding nests in different substrates: nests situated on bushes or on low broadleaved and evergreen trees are easier for humans to find and they may thus occur disproportionately in studies based on cold searching; when this method was complemented with radio-tagging the percentage of nests found on conifers and taller trees was much higher (cfr. Browne & Aebischer 2004, Arroyo *et al.* 2019).

However, and despite the potential effect of search methodologies on differences among studies, our review indicated marked geographical differences in the relative use of different substrates. Such differences may be explained by their relative availability. For example, extensive tree crops (almonds, olives) are commoner in southern Europe than in the north, and their proportion is even higher in North Africa; there, turtle dove nesting territories are mainly found in agricultural landscapes, mostly irrigated crops dominated by orange and olive groves (Hanane & Baamal 2011, Hanane & Besnard 2014, Kafi *et al.* 2015, Hanane 2016).

Additionally, differences in the risk of nest predation could explain the observed differences in nest substrates and characteristics of the nest: height, accessibility and exposure (Lormée 2015). The composition of predator communities varies spatially; while recorded predation was almost entirely by corvids in Britain (Murton 1968, Browne & Aebischer 2004, Browne *et al.* 2005), on continental Europe ground-based predators such as snakes and mammals also added to the guild, as did some birds of prey (Gaitzenauer 1990, Peiró 1990, Rocha & Hidalgo 2002, Dias 2016, Sáenz de Buruaga *et al.* 2016, Arroyo *et al.* 2019). A strategy to hide nests in closed environments, often protected by thorns, might be a good response to a predominantly avian predation risk, since avian predators generally detect breeding birds from above and based on visual cues (Engel *et al*. 2020). Nests are often protected by thorns and lianas in northern Europe, and this might be a measure to reduce predation from birds (Aubineau & Boutin 1998, Browne & Aebischer 2005, Lormée 2015). Ground-based predators, on the other hand, may use other cues to locate their prey, and the turtle dove strategy to reduce the probability of being detected and attacked by ground predators may be to distance their nest from the tree trunk, as it has been observed in Mediterranean environments (Dias 2016, Arroyo *et al.* 2019). Whether the choice of nest substrate is related to a hypothetical protection from predators remains to be assessed, however, as well as whether there is a connection between the type of nesting substrate and nest success. So far, there is no evidence that variation in nest failure might be driving population trends (Browne 2002, Browne & Aebischer 2004). In contrast, productivity (the number of offspring produced per female and breeding season) in this species might be rather based on the ability to quickly produce a replacement clutch after a failed attempt. The number of breeding attempts per season has been suggested to be dependent on body condition and ultimately on food availability (Browne 2002). Improving access to abundant food may be more critical than changing conditions at the nesting sites for boosting turtle dove populations, something that had been highlighted by the SAP (Fisher *et al.* 2018).

Importance of seeds of early-flowering wild plants

Across the range, turtle doves have been shown to consume a wide variety of plant species. The observed geographical variation in the plant species consumed suggests that the actual choice is probably dependant on what is locally and temporally variable, but overall our review highlights the importance of the seeds of wild plants, and particularly of those that flower early and provide seeds at the appropriate time for breeding (Figs. 2 & 3, Table 4).

During the first weeks after arrival to the breeding grounds, foraging will depend most heavily on wild seeds in all habitats, including woodland and farmland (Murton *et al.* 1964, Browne & Aebischer 2003a, Gutiérrez-Galán *et al.* 2019); crucially, during this time period, breeding pairs will have raised their first brood (Arroyo *et al.* 2019). The first generation of chicks must thus be fed primarily on natural seeds, except in the few places where, e.g., birds have access to spilt grain from farmyards being moved from the storage barns (Browne & Aebischer 2003a).

In several parts of the distribution range, it has been shown that there is a shift from wild seeds to cultivated seeds as the season progresses (Murton et al. 1964, Browne & Aebischer 2004, Browne et al. 2004, Dunn et al. 2015, 2018, Gutiérrez-Galán & Alonso 2016, Gutiérrez-Galán et al. 2019; Table 4). There is also a marked historical trend as the main diet has shifted from natural to cultivated seeds, particularly evident in places such as the UK, where changes in agricultural practices have reduced or removed many of the feeding opportunities available in the 1960s and 1970s (Browne & Aebischer 2001, 2004, Browne 2002). Because crop seeds are more nutritious than wild seeds (Díaz 1990), they are probably preferred when both food types are available; this happens from mid-June in southern Europe and progressively northwards.

A study by Rocha & Quillfeldt (2015) showed that sites where grain had been provided had a higher young/adult ratio among birds present in mid-August, leading to the interpretation that local breeding success could have been enhanced. However, those results could also indicate that juveniles forage more often where food is both abundant and predictable, even if (relatively) far from the breeding site. In other words, such results demonstrate use of anthropogenic food in late summer by juveniles and adults, in line with the home range studies, but they do not necessarily prove better breeding success. Additionally, Dunn et al. (2018) finding that the nestling condition of chicks fed with crop seeds was worse than those fed with wild seeds further emphasizes the benefits of favouring wild plants rather than providing crop seeds as supplementary food. Therefore, interventions to improve food availability should favour the provision of wild seeds rather than the provision of crop seeds.

Is there a link between migration phenology and food availability in the early season?

Given the importance of wild annual seeds highlighted in our review, these results suggest that migration phenology may be tuned to the availability of food on arrival from the wintering quarters. The turtle dove is one of the very few long-distance migrants that are also obligate granivores; of the 99 species of long-distance migratory birds in the Afro-Palaearctic system assessed by Moreau (1970), only two larks, three buntings, the Quail *Coturnix coturnix* and the turtle dove are wholly or largely dependent upon seeds; the other 92 species live on insects, some with a local and temporary supplement of berries. Compared to other Afro-Palaearctic bird species, the spring migration of the European Turtle Dove takes place relatively late in the season, with the bulk of birds arriving to the European shores between the end of April and early May. Irby (1875) and Brú (1913) already noticed this comparatively late phenology in the 19th century; the same pattern was observed through the 20th century (Bernis & Castroviejo 1968, Nankinov 1994, Urcun *et al.* 1995, Tryjanowski *et al.* 2002) and still continues at present (Fink *et al.* 2020). This late migration phenology may be an evolutionary adaptation to arrive to the breeding grounds when sufficient food is available, and not before.

Recommendations for habitat management to favour Turtle doves

As a globally-threatened species (BirdLife International 2019), the Turtle dove has justifiably received much attention from the conservation and scientific communities, who have proposed a number of practical habitat management measures aimed at reducing or reversing its ongoing population decline (Browne *et al.* 2004, Browne & Aebischer 2005, Bakaloudis *et al.* 2009, Dunn *et al.* 2015, Marx & Quillfeldt 2018). The internationally agreed Species Action Plan (Fisher *et al.* 2018) provides a list of recommendations for management with the objective to halt the species decline in the decade 2018-2028, and should be implemented as a matter of priority.

This review complements the Species Action Plan with a more specific analysis of habitat associations in the species. In particular, evidence of the association of breeding numbers with type of habitat, or with certain habitat features, allows making suggestions for potential habitat interventions to boost turtle dove densities. Such improvements could play an essential role in consolidating population growth when they are linked with measures to increase survival (for example, through hunting regulations). Our review indicates that the most efficient habitat management interventions would depend on the dominant landscape (farmland or woodland), but that overall those interventions should seek to increase the mixing of farmland and woodland, i.e., to augment the ecotone between them. In other words, management actions to favour turtle doves should aim to retain or recover elements of heterogeneity in the landscape, combining and integrating patches of farmland, grassland and forest in a mosaic pattern where possible. This means, in woodland, opening the canopy through thinning (if dense), creating forest clearings and preventing their subsequent encroachment; and on farmland, retaining or creating patches of shrub or areas with trees.

In all cases, it is important to ensure the provision of areas with high food availability, which is accessible for turtle doves, i.e. herbaceous grasslands with low vegetation height. Given the turtle dove’s specialised diet on seeds, and the importance of annuals in their diet (Fig.

4, Table 4), habitat management interventions aimed at increasing food availability at the beginning of the breeding period may allow earlier breeding and thus increased number of breeding attempts over the breeding period, something that forms the basis of conservation actions for the species in the UK (Browne & Aebischer 2004, Dunn & Morris 2012, Dunn *et al.* 2015, 2021). In southern latitudes, food availability in the early season may be less limiting. It is generally assumed that farmland intensification there is less acute, and ruderal plants are still widespread; at the same time, climate allows for early flowering (Fig. 3) in southern Europe. However, it would be critical to make sure that this is still the case, and to favour the proliferation of early-flowering wild plants, e.g., by maintaining grassy margins between farmland plots, keeping weedy tracks on farmland and woodland, as well as maintaining forest clearings through herbivory so they do not become encroached. Some of the studies in our review specifically suggest that maintaining extensive herbivory would be beneficial for this aim (particularly in forest), and this could be achieved either with wild ungulates or extensive livestock farming (Gutiérrez-Galán & Alonso 2016, Gutiérrez-Galán *et al.* 2019).

In summary, priority recommended actions in tree-dominated areas include:

- clear forest undergrowth to provide an open forest structure with only an herbaceous understorey; this can be part of fire prevention management
- maintain or introduce grazing in forest areas, by livestock or wild ungulates, at low densities and allowing for the proliferation of certain wildflowers (such as *Echium plantagineum* and *Amaranthus deflexus*) known to be part of the Turtle dove's diet

On the other hand, priority recommended actions on farmland-dominated areas include:

- maintain or promote elements of non-farmland habitats (natural grasslands, patches of forest, shrub)
- promote complex cultivation landscapes including grassy field margins and open areas (e.g., fallow land being ploughed in late winter) wherever possible
- after harvesting of cereal crops, retain stubble at least until October so that turtle doves have opportunities to feed on grain leftovers and ruderal plants growing in stubble (e.g., *Chenopodium album*); where grain storage occurs, allow birds to access spilt grain.

On both farmland and woodland landscapes, it would probably be useful to retain or open unpaved tracks with medium levels of disturbance (e.g., through public use) that allow for the proliferation of ruderal plants and other annuals in their margins, especially early-flowering ones, and to allow those plants to complete their full reproductive cycle and to offer seeds. Additionally, it would be necessary to ensure that enough suitable breeding habitat is available for Turtle doves, adapted to the local choice of nest site characteristics.

Conclusions

The Turtle dove is one of many migratory landbirds that are in decline in the Afro-Palaearctic system, many of which also have vast distribution ranges and therefore occupy also an ample selection of habitats. Our review highlights that for widespread species, knowledge on habitat associations obtained at a small part of their vast range may not be representative of what happens elsewhere and should not be generalised. When designing habitat interventions to promote the conservation of the species, it may therefore be necessary to have evidence of habitat relationships from a large part of the range. In the case of the turtle dove, most of the evidence analysed in this review comes from studies in the United Kingdom, France, Spain and Portugal and it focuses on the population that migrates along the western flyway (Marx *et al.* 2016, Fisher *et al.* 2018, Lormée *et al.* 2020). In contrast, a comparatively reduced number of studies are available for the central-eastern flyway population, which highlights the need for more evidence from that part of the range.

Finally, our review highlights that for the many declining species that favour the ecotone between woodland and farmland in the Afro-Palaearctic system, forestry and agricultural policies need to be combined to provide the right conditions. The case of the turtle dove provides compelling evidence that too much of any one thing (farmland or woodland) is detrimental to the abundance of the species, as is too little. Management interventions are needed in both tree-dominated and farmland-dominated landscapes, to provide for the combination of open forest interspersed with low grazing areas and complex cultivation systems with small parcels of mixed crop types, including woody permanent crops, where turtle dove populations have been shown to fare better. This may make it more complicated as more actors need to be involved. Also, it may make it more difficult to use certain resources (e.g. CAP funds) to provide exactly the right combination of measures needed in all places, as they may not necessarily be applicable in woodland. This realisation highlights the need to look for joint initiatives between forestry, farming and conservation to guarantee the continuation of sustainable practices and the preservation of biodiversity-rich areas in the human-dominated landscapes found across most of Europe.

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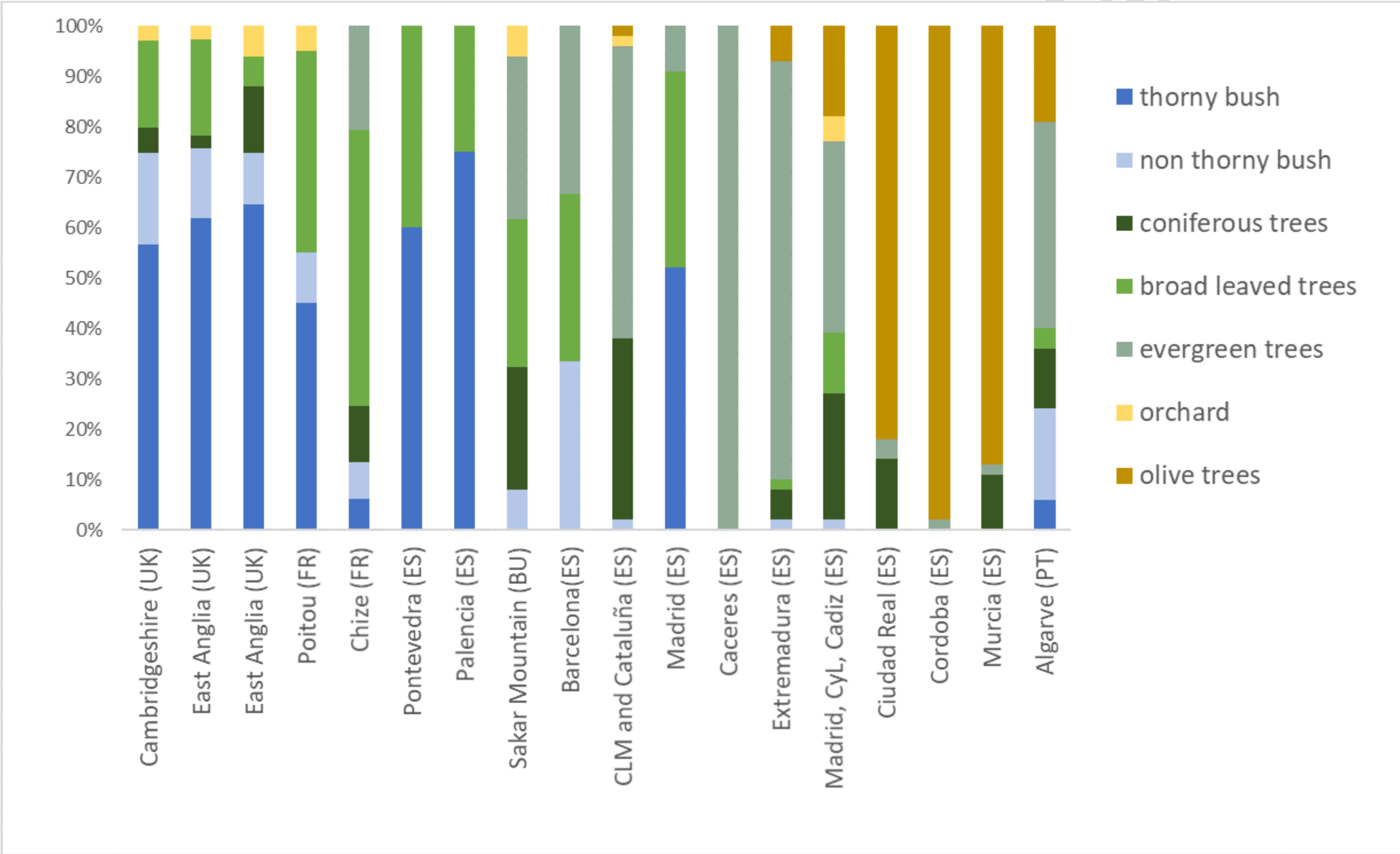
FIGURE LEGENDS.

Figure 1. Relative proportion of different nest substrates used by Turtle doves for nesting in different study sites in Europe. Locations are ranked by latitude along the x axis, from northernmost (left) to southernmost (right).

Figure 2. Proportion of plant species mentioned as food taken by turtle doves (Table 4) in relation to whether they are annual, biannual or perennial (A) or in relation to their type (B). In the latter, categories follow the classification developed by Dunn et al. (2018): "brassica" (any form of Brassicaceae plant family, either provisioned, cultivated or wild); "cultivated" (crop plants and seed mixes sown to provide seed for game or wild birds); "fed" (seed from anthropogenic source, such as bird tables); "wild" (any wild plant species).

Figure 3. Flowering phenology of plant species mentioned as turtle dove food in the Iberian Peninsula, Lines indicate the number of species that are described to have a peak flowering season in that month. Based on the information available on the project Flora-On website from the Portuguese Botanical Society, https://flora-on.pt.

FIGURES.



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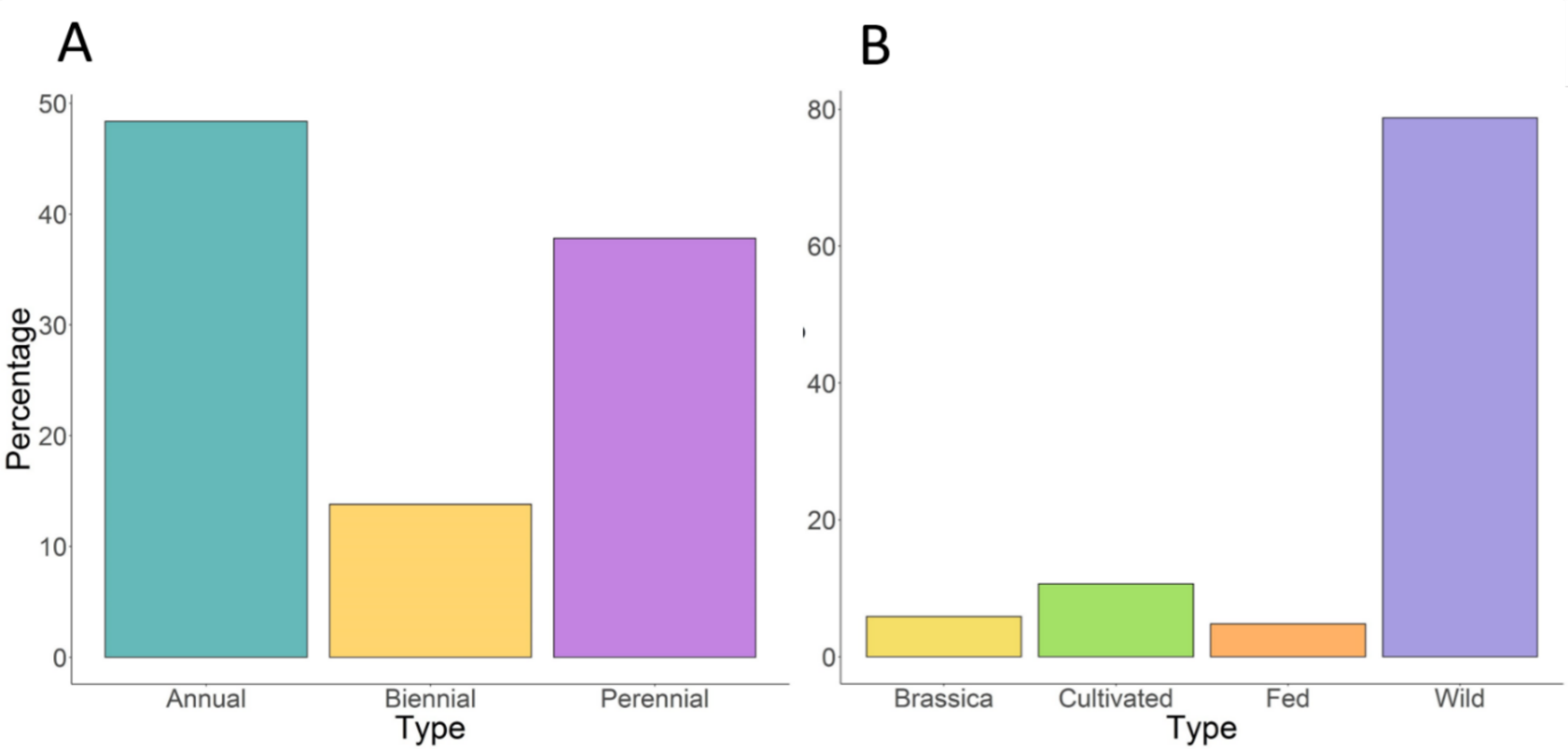

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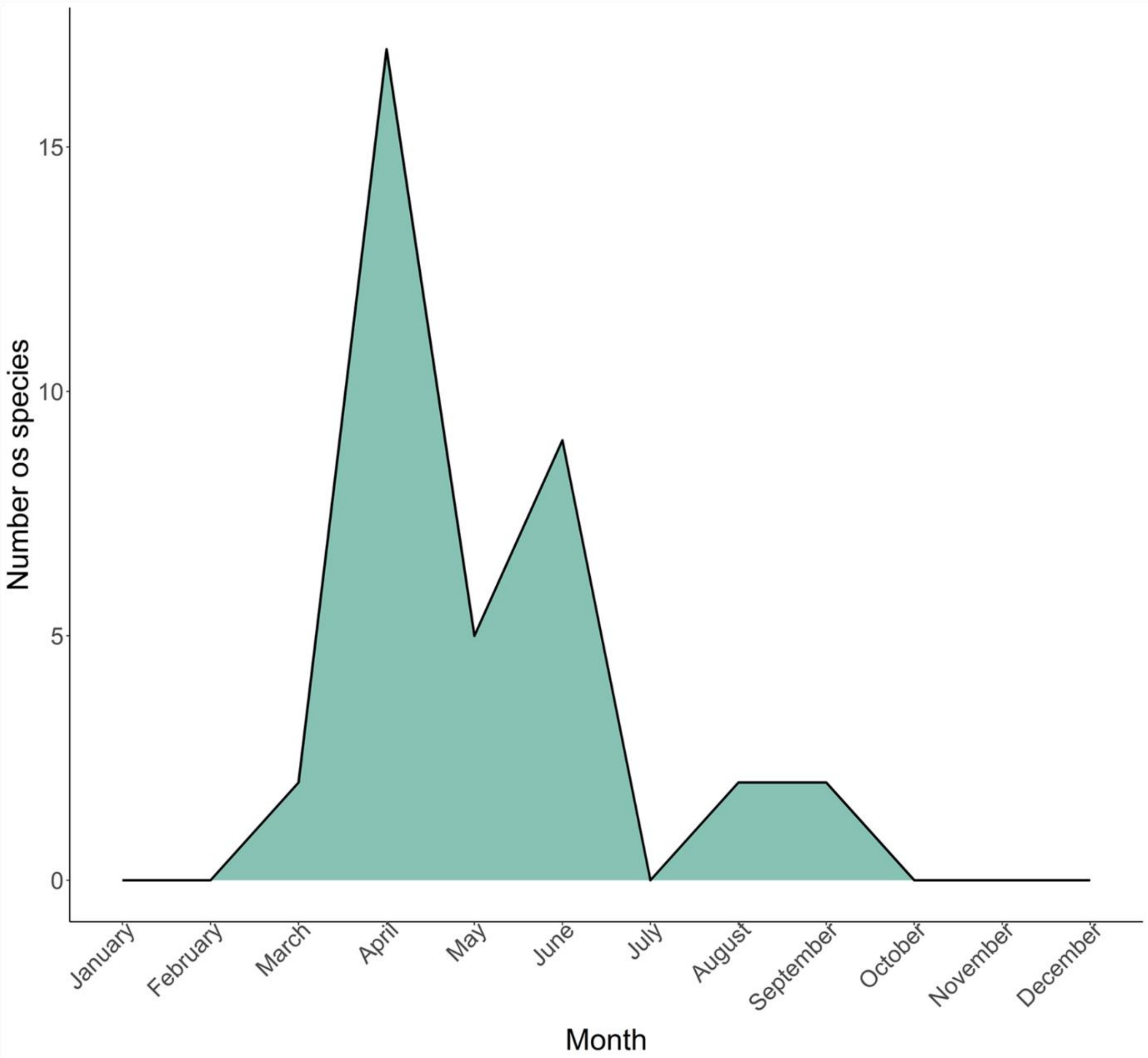

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Table 1a. Summary of main findings of the 32 studies reviewed that assessed the relationship between European Turtle Dove abundance (in the broad sense, including density, variation in numbers, etc.) and occurrence with habitat.

Area	Country	Study period	Variable analysed	Main Effect	Type	Reference
United Kingdom	UK	1960-1962 and 1966	nest abundance	Preferred habitat: ecotone where deciduous woodland gives way to open grassland. Fewer nests in conifer woodland and bushy heaths than expected from availability.	peer-reviewed paper	Murton 1968
United Kingdom	UK	<1990´s	review of previous literature	Densities of TD on farmland ca. half than in woodland during 1968-72. Within woodland habitats, TD favour scrub rather than pure woodland stands.	peer-reviewed paper	Browne & Aebischer 2005
United Kingdom	UK	1965-1995	territory density	Suitable woodland areas support densities up to 6.5 times higher than on farmland. On farmland, density positively related to the amount of hedgerow and woodland edge per unit area.	peer-reviewed paper	Browne *et al*. 2004
Kent	UK	1975-1984	territory density	After coppicing, TD numbers in a *Castanea silva* forest peaked at 14 years, following closure of canopy. By then, field layer had disappeared, and ground was bare.	peer-reviewed paper	Fuller & Moreton 1987
United Kingdom	UK	1988-1991	relative abundance	Higher abundance in 10km squares with higher proportion of farmland (>70%)	peer-reviewed paper	Fuller *et al*. 2004
United Kingdom	UK	1990-1992	occurrence probability	TD use of woodland positively influenced by habitat diversity (associations with shrubby vegetation) and negatively influenced by density of canopy	peer-reviewed paper	Hinsley *et al*. 1995
NE Essex	UK	1994-1996	territory density	Strong preferences for residential areas, scrub and woodland. Hedgerows used less often than expected.	peer-reviewed paper	Mason & Macdonald 2000
East Anglia	UK	1996	nest density	Nest density in a study area dominated by woodland higher than in another dominated by farmland	peer-reviewed paper	Calladine et al. 1997
SE England	UK	2008-2010	retained/lost territories and local abundance	TD more likely to be retained in sites with larger areas of established scrub and greater volumes of hedgerows, less likely in areas with grazed land. Abundance positively related to established area of scrub, volume of hedgerows and area of standing water	peer-reviewed paper	Dunn & Morris 2012
Essex, Suffolk, Cambridgeshire and Norfolk	UK	2011-2014	Territory density	Abundance of territorial TD declined more slowly on sites with accessible seed-rich intervention plots. Importance of non-farmed habitats (lightly grazed and semi-natural grassland, amenity land, fallows) for breeding TDs	peer-reviewed paper	Dunn et al. 2021
Knepp, W Sussex	UK	2012-2018	territory density	Number of territories increased from 0 to 16 following rewilding of former intensive farmland by allowing vegetation to grow freely and introducing herbivores and pigs; rootling effect of pigs shown to favour ruderal plants but effect on TD unproven	popular science; MSc thesis	Tree 2018; de Klee 2019

Zuidwest-Veluwe	NL	1977-1981	territory density	Highest densities found in conifer and mixed woodland and residential areas; intermediate densities in city gardens and low-scale farmland; lowest densities in floodplains, heaths and large-scale farmland	peer-reviewed paper	Biljsma 1985
Seewinkel	AT	1987-1989	nest density	In a context of farmland, nest density higher in thick shrub, dense or open forests with understorey, riparian forest and windbreaks than in open younger forests or forests without understorey.	peer-reviewed paper	Gaitzenauer 1990
Central-southern Bulgaria	BG	2016-2019	abundance	Higher density in riparian and oak forests, lower densities on farmland. Coniferous plantations and strips of trees on farmland used less often than expected from availability.	peer-reviewed paper	Gruychev 2020
Germany	DE	1998-1999 and 2013-2016	used/unused sites	Presence retained in areas with dense deciduous forest and middle age mixed forest, with more grassland and forest clearings	peer-reviewed paper	Kleemann & Quillfeldt 2014
Spain	ES	1989	nest density	Highest nest densities on two farmland areas including abundant almond or olive groves, and one farmland area with abundant shrub	report	Fernandez & Camacho 1989
Extremadura	ES	1996-1997	nest density	Nest density in wooded pastureland (dehesas) higher than in other habitats. Within dehesas, nest density increased with higher percentage of cultivated cereal, and where no herbicides applied.	book	Rocha & Hidalgo 2002
Andalucía	ES	1997-1998	abundance	Highest densities found in poplar plantations, followed by Mediterranean forest, olive groves and pine forest. Marginal farmland, upland heaths and Eucaliptus plantations had lowest densities.	popular science	Gutiérrez 2001
Catalonia	ES	1999-2002	abundance	Wildfire prevention works in Holm oak forest led to colonisation by TD when undergrowth cleared, and forest thinned out.	peer-reviewed paper	Camprodon & Brotons 2006
Alicante	ES	2001-2004	Presence/ abundance	TD presence favoured by shrub-pine mixed habitats in semi-arid, tree crops and pine forests, and extension of unpaved roads. Abundance only predicted by number of water bodies nearby.	PhD thesis	Bermúdez 2020
Basque Country	ES	2006	abundance	Density higher in riparian forests and in woodland than on farmland, but abundance in forest tended to decrease when tree cover >40%.	peer-reviewed paper	Sáenz de Buruaga et al. 2012
Catalonia	ES	2002-2011	abundance trends	TD abundance trends negatively related to farmland abandonment (shrub encroachment within farmland) but positively to % forest	peer-reviewed paper	Herrando et al. 2014
Catalonia	ES	2002-2013	abundance	TD abundance positively associated to % of forest.	peer-reviewed paper	Herrando et al. 2016
Jaén	ES	2014-2015	abundance	Local abundance in agroforest area higher in points closer to crops and with higher availability of wild seed cover.	peer-reviewed paper	Gutiérrez-Galán et al. 2018
Spain	ES	1996-2016	abundance and trends	Agricultural 10km squares had higher abundance (and less negative trends) than those with a higher proportion of woodland (more negative trends).	report	Carricondo 2016

Spain	ES	1996-2017	abundance trends	More negative trends in areas dominated by forest, 'dehesas', transitional woodland or sclerophyllous vegetation. Trends stable in areas dominated by olive orchards and positive in areas dominated by complex cultivation.	peer-reviewed paper	Moreno-Zarate et al. 2020
Vendée and Deux Sèvres	FR	1995-1997	territory density	Density of singing males correlated with length of hedges	conference proceedings	Aubineau & Boutin 1998
Hungary	HU	1999-2002	abundance and occupancy	Higher density in forest habitats, but habitat occupancy higher in mixed habitats (farmland and forest)	peer-reviewed paper	Szep et al. 2012
NE Greece	GR	2001-2002	used/unused sites	Used sites had higher canopy cover and higher density of medium size pine trees. Unused sites had higher density of mature pine trees.	peer-reviewed paper	Bakaloudis et al. 2009
Po Plain	IT	2015	occurrence	Occurrence probability higher in areas with high tree cover (semi-natural forests, poplar plantations) and areas with many shrubs and hedgerows. Areas with high proportion of crops were avoided	peer-reviewed paper	Chiatante et al. 2020
Portugal	PT	2002-2003	frequency of occurrence	Abundance positively related to broadleaved forests and pine stands without woody understorey. Also positive effect of the density of woody linear habitats and permanent crops (including olives/orchards)	peer-reviewed paper	Dias et al. 2013
Portugal	PT	2003-2004	territory density	In woodland areas, highest densities in pine forests or mixed stands, avoiding broadleaved stands, agroforestry areas or eucalyptus forests. In areas dominated by mosaic landscapes, highest densities in orchards and vineyards, riparian galleries and shrubs.	PhD thesis	Dias 2016

Table 1b. Summary of main findings of the 32 studies reviewed that assessed the relationship between European Turtle Dove abundance (in the broad sense, including density, variation in numbers, etc.) and occurrence with habitat. Results of direct comparison between habitats, and favourable elements in each major habitat type.

Reference	Country	Preferred habitat	Favourable elements (woodland)	Favourable elements (farmland)
Murton 1968	UK	Forest–Farmland ecotone	Broadleaved > coniferous	
Browne & Aebischer 2005	UK	Woodland > Farmland	Scrub	
Browne et al. 2004	UK	Woodland > Farmland		Hedge and woodland edge
Fuller & Moreton 1997	UK		Closed canopy, but intermediate age > mature forest	
Fuller 2004		Farmland > Woodland		
Hinsley et al. 1995	UK		Structure diversity and open canopy	
Mason & Macdonald 2000	UK	Residential areas > Farmland		
Calladine et al. 1997	UK	Woodland > Farmland		
Dunn & Morris 2012	UK			Scrub and hedgerows 4 m tall, bare ground and fallow > grazed lands
Dunn et al. 2021	UK			Fallows, semi-natural grassland, amenity lands
Tree 2018; de Klee 2019	UK			Patches of natural woodland and scrub
Biljsma 1985	NL	Woodland > Farmland		
Gaitzenauer 1990	AT		Dense > Open	Patches of natural woodland and scrub
Gruychev 2020	BG	Riparian > Woodland > Farmland		
Kleemann & Quillfeldt 2014	DE	Woodland > Farmland	Grasslands and clearings. Dense deciduous and middle-aged mixed forests	
Fernandez & Camacho 1989	ES	Farmland > Woodland and shrub		Tree crops, shrub
Rocha & Hidalgo 2002	ES	Wooded pastureland > Farmland	Proximity to cereal crops	No herbicides
Gutierrez 2001	ES	Woodland > Farmland		Olive groves
Camprodon & Brotons 2006	ES		Open (clearing and thinning) > Dense	
Bermudez 2020	ES		Water bodies	Tree crops, water bodies
Saenz de Buruaga et al. 2012	ES	Riparian > Woodland > Farmland	Lower tree cover	Hedgerows
Herrando et al. 2014	ES			Rediced shrub encroachment
Herrando et al. 2016	ES	Woodland > Farmland		
Gutierrez-Galan et al. 2018	ES		Proximity to cereal crops and open areas with weeds	

Carricondo 2016	ES	Farmland > Woodland		
Moreno-Zarate et al. 2020	ES			Tree crops and mixed crops
Aubineau & Boutin 1998	FR			Hedge density
Szep et al. 2012	HU	Woodland > Farmland	Farmland in vicinity	
Bakaloudis et al. 2009	GR		Higher canopy cover. Medium size > mature pine trees	
Chiatante et al. 2020	IT	Riparian, tree plantations and Woodland > Farmland		Hedgerow density
Dias et al. 2013	PT	Woodland > Riparian > Farmland	Open > Dense. No woody understory	Tree crops
Dias 2016	PT	Woodland > Farmland	Conifer> Broadleaved	Orchards, shrubs

Table 2. Summary of main findings of studies assessing the habitat structure of areas where turtle doves occur, ranked up, where possible, following the order of preference shown by the species (i.e. habitat 1 was where the highest abundance or preference was recorded). 'Landscape' is the dominant cover of surrounding land, as shown by CORINE land cover map available for the year nearest to study period (FA = farmland; ML = mixed landscape; FO = forest). 'Canopy' cover follows the FAO Land Cover Classification System http://www.fao.org/3/x0596e/X0596e01n.htm (C = closed (more than 60-70 percent); O = open (60-70 percent to 10-20 percent); S = sparse (10-20 percent to 1 percent); L = linear woody structure (riparian forest, windbreak, hedgerow, bocage). 'Understorey' describes the structure of the underlying layer of vegetation (H = herbaceous; W = woody; B = bare soil; FF = forest floor (leaves, detritus, etc.)). 'Herbivory' describes whether grazing/browsing occurs, and which animals are involved (● = wild animals; ○ = livestock). For each category, a grey cell indicates inferred information (e.g., from pictures of the area, etc.) rather than provided in the publication.

HABITAT 1	Landscape	canopy	understorey	herbivory	HABITAT 2	Landscape	canopy	understorey	herbivory	HABITAT 3	Landscape	canopy	understorey	herbivory	HABITAT 4	Landscape	cnopy	understorey	herbivory	COUNTRY	REFERENCE
SEMI-NATURAL LANDSCAPES (where non-farmland component of the landscape predominant, or the unmanaged area within the farmland landscape is la																					
Mediterranean mixed forest	FO	O	H	●																ES	Camprodon & Brotons 2006
Conifer	ML	O	H	●	Mixed forest	ML	O	H	●											GR	Bakaloudis et al. 2009
Broadleaved	ML	O	H	○●																UK	Tree 2018, Klee 2019
Woody linear (riparian)	ML	L	n/a		Broadleaved	ML	O	H	●	Conifer	ML	n/a	H	●	Shrubland	ML	n/a	n/a	●	BG	Gruychev 2020
Mediterranean mixed forest	ML	O	H	●	Mediterranean mixed forest	FO	O	H	●											ES	Gutiérrez-Galán et al. 2018
SEMI-TRANSFORMED LANDSCAPES (areas where farmland is mixed with unmanaged forested areas at the landscape level)																					
Agroforestry (dehesa)	ML	O	H	○	Permanent crops (olive)	ML	O	H		Mediterranean mixed forest	ML	n/a	n/a	●	Woody linear (riparian)	ML	S	n/a		ES	Rocha & Hidalgo 2002
Semi-arid mixed shrub-pine woodland	ML	O	B	●	Permanent crops (almond, citrus)	ML	O	H		Conifer forest	FO	O	n/a	●						ES	Bermúdez 2020
Woody linear (riparian)	ML	L	n/a		Evergreen oak forest w crops	ML	O	H		Shrubland	ML	O	W		Farmland / pasture	ML	S	H	○	ES	Sáenz de Buruaga et al. 2012
Broadleaved	ML	n/a	n/a		Miscellaneous	ML	n/a	n/a		Pasture	ML	n/a	n/a	○	Arable land	ML	O	H		UK	Browne 2002, Browne & Aebischer 2003, Browne et al. 2004

Broadleaved (schlerophyll)	ML	O	H	●	Conifer	ML	C	H	●	Permanent crops	ML	O	H		Woody linear (riparian, hedgerows)	ML	L	n/a		PT	Dias et al. 2013, Dias 2016
HIGHLY TRANSFORMED LANDSCAPES (where farmland component of the landscape is clearly predominant, and wooded/unmanaged elements are small or isolated)																					
Mixed forests	ML	C	n/a	○●	Conifer	ML	C	n/a	○●	Residential area	ML	O	H		Built-up area	ML	O	H		NL	Bijlsma 1985
Shrubland	FA	C	W	○	Broadleaved	FA	C	W	○	Broadleaved	FA	O	W	○	Woody linear (windbreaks, riparian)	FA	C	W	○	AT	Gaitzenauer 1990
Broadleaved	ML	C	FF	●																UK	Fuller & Moreton 1987
Residential area	FA	O	H		Woody linear (hedgerow)	FA	L	W		Broadleaved	FA	n/a	n/a		Shrubland	FA	C	W		UK	Mason & Macdonald 2000
Miscellaneous	FA	n/a	n/a		Pasture	FA	O	H	○	Broadleaved	FA	n/a	n/a		Arable land	FA	O	H		UK	Browne 2002, Browne & Aebischer 2003, Browne et al. 2004
Woodland	FA	O	W																	UK	Hinsley et al. 1995
Mixed forest	FA	T	W	●	Broadleaved	FA	C	H	●	Pasture	FA	O	W	○	Shrubland	FA	C	W		DE	Kleemann & Quillfeldt 2014
Agroforestry ("bocage")	FA	L	H	○																FR	Lormée 2015
Conifer (plantation)	ML	C	FF		Woody linear (hedgerow)	ML	C	W												UK	Baines 2019
Broadleaved (poplar plantations)	FA	C	H		Riparian forests	FA	L	n/a		Shrubland	FA	C	W		Woody linear (hedgerow)	FA	L	W		IT	Chiatante et al. 2020

N.B: The study by Browne (2002), Browne & Aebischer (2003) and Browne et al. (2004) appears twice because it compared habitat use in two study areas within different landscapes.

Table 3. Summary of studies providing quantitative information on the use of nest substrates by Turtle Doves in Europe.

Country / region	Study year	Nests	Substrates used	Study type	Reference
UK	1962-1966	511	43% *Crataegus monogyna*, 17% *Sambucus nigra*, 6% *Prunus spinosa*, 6% wild rose or bramble, 5% Salix, 12% other deciduous trees, 5% conifers, 3% orchards or ornamental trees, 1% *Ilex aquifolium*, 1% *Hedera helix* and *lonicera periclymenum*, 1% *Ulex europaeus*.	peer-reviewed paper	Murton 1968
East Anglia (UK)	1996	31	65% *Crataegus monogyna*, 16% *Sambucus nigra*, 6% *Prunus spinosa*, 3% *Acer pseudoplatanus*, *Picea albies*, *Malus silvestris*, *Ulmus glabra*	report	Calladine et al. 1997
East Anglia (UK)	1998-2000	143	64% thorny bushes, 13% coniferous trees, 10% Elder, 6% broadleaved trees, 6% fruit trees	peer-reviewed paper	Browne & Aebischer 2004
Poitou (FR)	1990´s	59	35% *Crataegus monogyna*, 30% *Coryllus avellana*, 10% *Prunus spinosa*, 5% *Acer campestre*, 5% *Euonymus europaeus*, 5% *Pyrus communis*, 5% *Salix caprea*, 5% *Sambucus nigra*	conference proceedings	Aubineau & Boutin 1998
France	2000´s		108 species used, but *Crataegus monogyna*, *Prunus spinosa* and *Sambucus nigra* particularly favoured	popular science	Lormée 2015
Bulgaria	2014-2016	37	24% *Pinus nigra*, 16% *Quercus cerris*, 16% *Quercus pubescens*, 8% *Ulmus minor*, 8% *Acer negundo*, 8% *Paliurus spina-christi*, 8% *Salix sp.*; 6% *Pyrus*, 5% *Robinia pseudocacacia*	peer-reviewed paper	Gruychev 2017
Pontevedra (ES)	1989	5	40% *Rubus ulmifoluis*, 20% *Betula celtiberica*, 20% *Crataegus monogyna*, 20% *Salix*	report	Fernandez & Camacho 1989
Palencia (ES)	1989	11	54% *Rosa canina*, 18% *Rubus ulmifolius*, 9% *Crataegus monogyna*, 9% *Salix*, 9% *Ulmus*	report	Fernandez & Camacho 1989
Barcelona(ES)	1989	3	33.3% *Juniperus oxycedrus*,33.3% *Quercus faginea*, 33.3% *Rubus ulmifolius*	report	Fernandez & Camacho 1989
Madrid (ES)	1989	21	33% *Rubus ulmifolius*, 19% *Crataegus monogyna*, 19% *Salix*, 15% *Ulmus minor*, 9% *Quercus rotundifolia*, 5% *Populus nigra*	report	Fernandez & Camacho 1989
Ciudad Real (ES)	1989	51	82% *Olea europaea*, 14% *Pinus halepensis*, 4% *Ceratonia siliqua*	report	Fernandez & Camacho 1989
Caceres (ES)	1989	48	100% *Quercus rotundifolia*	report	Fernandez & Camacho 1989
Cordoba (ES)	1989	68	98% *Olea europaea*, 2% *Quercus rotundifolia*	report	Fernandez & Camacho 1989
Murcia (ES)	1989	52	87% *Olea europaea*, 11% *Pinus halepensis*, 2% *Ceratonia siliqua*	report	Fernandez & Camacho 1989
Extremadura (ES)	1996-1997	325	76% *Quercus ilex rotundifolia*; 7% *Olea europaea*, 6% *Pinus sp.*, 3% *Quercus suber*, 2% *Eucaliptus sp.*, <2% *Fraxinus excelsior*, *Ficus carica*, *Quercus faginea*, *Populus nigra*, *Alnus glutinosa*, *Salix*, *Quercus pyrenaica*, *Populus alba*, *Arbutus unedo*	book	Rocha & Hidalgo 2002

Spain	2012-2013	45	25% *Pinus sp*., 18% *Olea europaea*, 18% *Quercus ilex*, 14% *Quercus pyrenaica*, 12% *Fraxinus angustifolia*, <5% *Prunus dulcis*, *Quercus coccifera*, *Juniperus sp*., *Quercus faginea*, *Quercus coccifera*	report	Sáenz de Buruaga et al. 2013
Castilla la Mancha and Cataluña (ES)	2018-2019	64	56% *Quercus sp*., 36% *Pinus sp*., 4% *Olea europaea* and *Prunus dulcis*, 1% *Arbutus unedo*, 1% *Juniperus oxycedrus*	conference poster	Arroyo et al. 2019
Algarve (PT)	2003-2004	84	41% *Quercus sp*., 19% *Olea europaea* and *Prunus dulcis*, 12% coniferous trees, 4% broad-leaved trees, 6% thorny bushes, 18% other bushes	conference poster	Dias & Rego 2017

Table 4. Plant species whose seeds have been reported as ingested by Turtle Dove.

Taxonomic unit	Family	Grown	Annual	Bien-nial	Peren-nial	References
Abies alba	Pinaceaea	Wild			●	Bijlsma (1985)
Acer campestre	Sapindaceaea	Wild			●	Dunn et al. (2018)
Achillea millefolium	Asteraceae	Wild			●	Dunn et al. (2018)
Agropyron sp.	Poaceae	Wild			●	Murton et al. (1964)
Agrostis sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Agrostis stolonifera	Poaceae	Wild			●	Dunn et al. (2018)
Alopecurus myosuroides	Poaceae	Wild	●			Dunn et al. (2018)
Alopecurus sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Amaranthus blitoides	Amaranthaceae	Wild	●			Kiss et al. (1978)
Amaranthus deflexus	Amaranthaceae	Wild	●	●	●	Gutiérrez-Galán & Alonso (2016)
Amaranthus retroflexus	Amaranthaceae	Wild	●			Kiss et al. (1978)
Amaranthus sp.	Amaranthaceae	Wild	●			Jiménez et al. (1992), Dias & Fontoura (1996), Dunn et al. (2018)
Anagallis arvensis	Primulaceae	Wild	●	●		Murton et al. (1964), Dunn et al. (2018)
Anagallis sp.	Primulaceae	Wild	●	●	●	Dunn et al. (2018)
Anthemis cotula	Asteraceae	Wild	●			Murton et al. (1964), Dunn et al. (2018)
Anthriscus sp.	Apiaceae	Wild		●	●	Dunn et al. (2018)
Apiaceae	Apiaceae	Wild	●		●	Dunn et al. (2018)
Arrhenatherum elatius	Poaceae	Wild			●	Dunn et al. (2018)
Artemisia vulgaris	Asteraceae	Wild			●	Dunn et al. (2018)
Asperula sp.	Rubiaceae	Wild	●		●	Gutiérrez-Galán & Alonso (2016)
Asteraceae	Asteraceae	Wild	●	●	●	Dunn et al. (2018)
Atriplex sp.	Amaranthaceae	Wild	●		●	Dunn et al. (2018)
Atriplex patula	Amaranthaceae	Wild	●			Murton et al. (1964), Browne & Aebischer (2003)
Avena fatua	Poaceae	Wild	●			Calladine et al. (1997)
Avena sp.	Poaceae	Wild	●			Dunn et al. (2018)
Bellis perennis	Asteraceae	Wild	●		●	Dunn et al. (2018)
Boraginaceae	Boraginaceae	Wild	●	●	●	Dunn et al. (2018)
Borago officinalis	Boraginaceae	Wild	●			Dunn et al. (2018)
Brassica carinata	Brassicaceae	Brassica	●			Dunn et al. (2018)
Brassica juncea	Brassicaceae	Brassica	●			Dunn et al. (2018)
Brassica napus	Brassicaceae	Brassica	●	●		Murton et al. (1964), Calladine et al. (1997), Browne & Aebischer (2003), Dunn et al. (2018)
Brassica oleracea	Brassicaceae	Brassica		●	●	Dunn et al. (2018)
Brassica rapa	Brassicaceae	Brassica	●	●		Dunn et al. (2018)

Brassica sp.	Brassicaceae	Brassica	●	●	●	Jiménez et al. (1992), Dias & Fontoura (1996), Dunn et al. (2018)
Brassicaceae	Brassicaceae	Brassica	●	●	●	Bijlsma (1985), Dunn et al. (2018)
Calendula arvensis	Asteraceae	Wild	●	●		Gutiérrez-Galán & Alonso (2016)
Calystegia sepium	Convolvulaceae	Wild			●	Dunn et al. (2018)
Cannabis sativa	Cannabaceae	Fed	●			Dunn et al. (2018)
Capsella bursa-pastoris	Brassicaceae	Brassica	●	●		Dunn et al. (2018)
Carthamus glaucus	Asteraceae	Wild	●			Dunn et al. (2018)
Carthamus sp.	Asteraceae	Wild	●			Dunn et al. (2018)
Carthamus tinctorius	Asteraceae	Fed	●			Dunn et al. (2018)
Caryophyllaceae	Caryophyllaceae	Wild	●		●	Dunn et al. (2018)
Cenchrus americanus	Poaceae	Fed	●			Dunn et al. (2018)
Centaurea sp.	Asteraceae	Wild	●		●	Dunn et al. (2018)
Cerastium fontanum	Caryophyllaceae	Wild		●	●	Dunn et al. (2015)
Cerastium glomeratum	Caryophyllaceae	Wild	●			Dunn et al. (2018)
Cerastium holosteoides	Caryophyllaceae	Wild			●	Murton et al. (1964)
Chamaecyparis lawsoniana	Cupressaceaea	Cultivated			●	Dunn et al. (2018)
Chenopodium album	Amaranthaceae	Wild	●			Murton et al. (1964), Dunn et al. (2018)
Chenopodium polyspermum	Amaranthaceae	Wild	●			Dunn et al. (2018)
Chenopodium sp.	Amaranthaceae	Wild	●		●	Jiménez et al. (1992), Dias & Fontoura (1996), Dunn et al. (2018)
Chromolaena odorata	Asteraceae	Wild			●	Dunn et al. (2018)
Chrozophora tinctoria	Euphorbiaceae	Wild	●			Jiménez et al. (1992), Gutiérrez-Galán & Alonso (2016)
Cirsium arvense	Asteraceae	Wild			●	Dunn et al. (2018)
Cirsium velatum	Asteraceae	Wild			●	Dunn et al. (2018)
Cirsium vulgare	Asteraceae	Wild		●		Dunn et al. (2018)
Citrus sp.	Rutaceaea	Cultivated			●	Dunn et al. (2018)
Clematis vitalba	Ranunculaceae	Wild			●	Dunn et al. (2018)
Convolvulus arvensis	Convolvulaceae	Wild			●	Gutiérrez-Galán & Alonso (2016)
Convolvulus sp.	Convolvulaceae	Wild	●		●	Jiménez et al. (1992), Dias & Fontoura (1996)
Corydalis (=Ceratocapnos) claviculata	Papaveraceae	Wild	●			Bijlsma (1985)
Crassulaceae	Crassulaceaea	Wild	●	●	●	Dunn et al. (2018)
Cucumis sp.	Cucurbitaceae	Cultivated	●		●	Dunn et al. (2018)
Cucurbitaceae	Cucurbitaceae	Cultivated	●		●	Dunn et al. (2018)
Cynara humilis	Carduoideae	Wild			●	Gutiérrez-Galán & Alonso (2016)
Dactylis glomerata	Poaceae	Wild			●	Dunn et al. (2018)
Dactyloctenium aegyptium	Poaceae	Wild	●			Dunn et al. (2018)
Deschampsia flexuosa	Poaceae	Wild	●			Bijlsma (1985)

Echium plantagineum	Boraginaceae	Wild	●	●		Murton et al. (1964), Gutiérrez-Galán & Alonso (2016)
Elymus repens	Poaceae	Wild			●	Dunn et al. (2018)
Epilobium sp.	Onagraceaea	Wild	●		●	Dunn et al. (2018)
Euphorbiaceae	Euphorbiaceae	Wild	●	●	●	Dunn et al. (2018)
Euphorbia sp.	Euphorbiaceae	Wild	●	●	●	Murton et al. (1964)
Festuca sp.	Poaceae	Wild			●	Murton et al. (1964), Dunn et al. (2018)
Fumaria officinalis	Papaveraceae	Wild	●			Browne & Aebischer (2003), Dunn et al. (2015)
Fumaria sp.	Papaveraceae	Wild	●			Murton et al. (1964), Dias & Fontoura (1996)
Galium aparine	Rubiaceaea	Wild	●			Murton et al. (1964), Dunn et al. (2018)
Geraniaceae	Geraniaceae	Wild	●		●	Dunn et al. (2018)
Geranium dissectum	Geraniaceae	Wild	●			Dunn et al. (2018)
Geranium lucidum	Geraniaceae	Wild		●		Dunn et al. (2018)
Geranium molle	Geraniaceae	Wild	●			Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Geranium pusillum	Geraniaceae	Wild	●			Dunn et al. (2018)
Geum urbanum	Rosaceae	Wild			●	Dunn et al. (2018)
Guizotia abyssinica	Asteraceae	Fed	●			Dunn et al. (2018)
Helianthemum sp.	Cistaceae	Wild	●		●	Jiménez et al. (1992)
Helianthus annuus	Asteraceae	Fed	●			Kiss et al. (1978), Jiménez et al. (1992), Dias & Fontoura (1996), Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Helianthus argophyllus	Asteraceae	Fed	●			Dunn et al. (2018)
Helminthotheca echioides	Asteraceae	Wild	●		●	Dunn et al. (2018)
Holcus lanatus	Poaceae	Wild			●	Dunn et al. (2018)
Holcus sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Hordeum sp.	Poaceae	Cultivated	●		●	Dunn et al. (2018)
Hordeum vulgare	Poaceae	Cultivated	●			Jiménez et al. (1992), Dias & Fontoura (1996), Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Hypecoum sp.	Papaveraceae	Wild	●			Dias & Fontoura (1996)
Jacobaea vulgaris	Asteraceae	Wild		●		Dunn et al. (2018)
Kickxia spuria	Plantaginaceae	Wild	●			Murton et al. (1964)
Larix decidua	Pinaceaea	Wild			●	Bijlsma (1985)
Lathyrus sp.	Fabaceae	Wild	●		●	Dias & Fontoura (1996)
Linum usitatissimum	Linaceaea	Cultivated	●			Calladine et al. (1997)
Linum sp.	Linaceaea	Cultivated	●	●	●	Dunn et al. (2018)
Lolium sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Malva sp.	Malvaceae	Wild	●		●	Gutiérrez-Galán & Alonso (2016)
Medicago lupulina	Fabaceae	Wild	●		●	Dunn et al. (2015)

Medicago sp.	Fabaceae	Wild	●		●	Murton et al. (1964), Dias & Fontoura (1996)
Melilotus sp.	Fabaceae	Wild	●	●		Dias & Fontoura (1996)
Ornithopus compressus	Fabaceae	Wild	●			Gutiérrez-Galán & Alonso (2016)
Panicum miliaceum	Poaceae	Fed	●			Dunn et al. (2018)
Papaver rhoeas	Papaveraceae	Wild	●			Dunn et al. (2018)
Papaver sp.	Papaveraceae	Wild	●	●	●	Dias & Fontoura (1996)
Pastinaca sativa	Apiaceae	Cultivated		●	●	Dunn et al. (2018)
Pennisetum glaucum	Poaceae	Cultivated	●			Kiss et al. (1978)
Persicaria lapathifolia	Polygonaceaea	Wild	●			Dunn et al. (2018)
Persicaria maculosa	Polygonaceae	Wild	●			Browne & Aebischer (2003)
Phalaris sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Picea abies	Pinaceaea	Wild			●	Bijlsma (1985)
Pinus sp.	Pinaceaea	Wild			●	Dunn et al. (2018)
Pinus sylvestris	Pinaceaea	Wild			●	Bijlsma (1985)
Pisum sativum	Fabaceae	Cultivated	●			Dunn et al. (2018)
Plantago lanceolata	Plantaginaceae	Wild			●	Dunn et al. (2018)
Poa annua	Poaceae	Wild	●			Dunn et al. (2018)
Poa infirma	Poaceae	Wild	●			Dunn et al. (2018)
Poa sp.	Poaceae	Wild	●		●	Dunn et al. (2018)
Poa trivialis	Poaceae	Wild			●	Dunn et al. (2018)
Poaceae	Poaceae	Wild	●		●	Dunn et al. (2018)
Polygonum aviculare	Polygonaceae	Wild	●			Browne & Aebischer (2003)
Polygonum lapathifolium	Polygonaceae	Wild	●			Gutiérrez-Galán & Alonso (2016)
Polygonum sp.	Polygonaceae	Wild	●		●	Murton et al. (1964), Kiss et al. (1978)
Potentilla sp.	Rosaceae	Wild	●	●	●	Dunn et al. (2018)
Primulaceae	Primulaceae	Wild	●		●	Dunn et al. (2018)
Prunus sp.	Rosaceae	Wild			●	Dunn et al. (2018)
Ranunculus repens	Ranunculaceae	Wild			●	Murton et al. (1964), Calladine et al. (1997)
Ranunculus sp.	Ranunculaceae	Wild	●		●	Gutiérrez-Galán & Alonso (2016)
Raphanus raphanistrum	Brassicaceae	Wild	●			Gutiérrez-Galán & Alonso (2016)
Raphanus sativus	Brassicaceae	Cultivated	●	●		Dunn et al. (2018)
Reseda lutea	Resedaceae	Wild	●	●	●	Murton et al. (1964), Browne & Aebischer (2003)
Retama sphaerocarpa	Fabaceae	Wild			●	Jiménez et al. (1992)
Rorippa sylvestris	Brassicaceae	Brassica			●	Dunn et al. (2018)
Rosa sp.	Rosaceae	Wild			●	Dunn et al. (2018)
Rosaceae	Rosaceae	Wild	●		●	Dunn et al. (2018)
Rubus sp.	Rosaceae	Wild			●	Dunn et al. (2018)
Rumex acetosella	Polygonaceae	Wild			●	Bijlsma (1985)
Rumex crispus	Polygonaceae	Wild			●	Dias & Fontoura (1996)

Rumex sp.	Polygonaceae	Wild	●		●	Murton et al. (1964), Dias & Fontoura (1996), Gutiérrez-Galán & Alonso (2016)
Salicornia sp.	Amaranthaceae	Wild	●			Dunn et al. (2018)
Salsola kali	Amaranthaceae	Wild	●			Gutiérrez-Galán & Alonso (2016)
Sambucus nigra	Adoxaceaea	Wild			●	Dunn et al. (2018)
Senecio vulgaris	Asteraceae	Wild	●			Dunn et al. (2018)
Setaria viridis	Poaceae	Wild	●			Kiss et al. (1978)
Silene alba	Caryophyllaceae	Wild	●	●	●	Murton et al. (1964)
Silene vulgaris	Caryophyllaceae	Wild			●	Murton et al. (1964)
Silene sp.	Caryophyllaceae	Wild	●	●	●	Gutiérrez-Galán & Alonso (2016)
Sinapis sp.	Brassicaceae	Brassica	●			Murton et al. (1964)
Sonchus arvensis	Asteraceae	Wild			●	Dunn et al. (2018)
Sorghum sp.	Poaceae	Fed	●		●	Dunn et al. (2018)
Spergula arvensis	Caryophyllaceae	Wild	●			Murton et al. (1964)
Spergula vernalis	Caryophyllaceae	Wild	●			Bijlsma (1985)
Stellaria media	Caryophyllaceae	Wild	●	●	●	Murton et al (1964), Bijlsma (1985), Calladine et al. (1997), Browne & Aebsicher (2003), Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Stellaria neglecta	Caryophyllaceae	Wild	●	●		Dunn et al. (2018)
Stellaria pallida	Caryophyllaceae	Wild	●	●		Dunn et al. (2018)
Stellaria sp.	Caryophyllaceae	Wild	●	●	●	Murton et al. (1964)
Suaeda maritima	Amaranthaceae	Wild			●	Dunn et al. (2018)
Suaeda sp.	Amaranthaceae	Wild	●		●	Dunn et al. (2018)
Silybum marianum	Asteraceae	Wild	●	●		Gutiérrez-Galán & Alonso (2016)
Symphytum sp.	Boraginaceae	Wild			●	Dunn et al. (2018)
Thlaspi arvense	Brassicaceae	Brassica	●			Dunn et al. (2018)
Trifolium pratense	Fabaceae	Wild	●		●	Dunn et al. (2015)
Trifolium repens	Fabaceae	Wild			●	Dunn et al. (2015)
Trifolium sp.	Fabaceae	Wild	●		●	Murton et al. (1964)
Trifolium stellatum	Fabaceae	Wild	●			Gutiérrez-Galán & Alonso (2016)
Tripleurospermum maritimum	Asteraceae	Wild	●			Dunn et al. (2018)
Triticeae	Poaceae	Cultivated	●			Dunn et al. (2018)
Triticum aestivum	Poaceae	Cultivated	●			Murton et al. (1964), Kiss et al. (1978), Jiménez et al. (1992), Calladine et al. (1997), Browne & Aebischer (2003), Dunn et al. (2018)
Triticum sp.	Poaceae	Cultivated	●			Dias & Fontoura (1996), Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Tussilago farfara	Asteraceae	Wild			●	Dunn et al. (2018)

Urtica dioica	Urticaceae	Wild			●	Browne & Aebischer (2003), Dunn et al. (2018)
Urtica urens	Urticaceae	Wild	●			Calladine et al. (1997)
Valerianella sp.	Caprifoliaceae	Wild	●	●		Dias & Fontoura (1996)
Vicia hirsuta	Fabaceae	Cultivated	●			Dunn et al. (2018)
Vicia sp.	Fabaceae	Wild	●		●	Kiss et al. (1978), Dias & Fontoura (1996), Gutiérrez-Galán & Alonso (2016)
Vicia sativa	Fabaceae	Cultivated	●			Murton et al (1964), Jiménez et al. (1992), Browne & Aebsicher (2003), Dunn et al. (2015), Gutiérrez-Galán & Alonso (2016), Dunn et al. (2018)
Viola arvensis	Violaceae	Wild	●	●		Browne & Aebischer (2003), Dunn et al. (2018)
Viola tricolor	Violaceae	Wild	●	●	●	Murton et al. (1964)
Violaceae	Violaceae	Wild	●		●	Dunn et al. (2018)
Zea mays	Poaceae	Fed	●			Gutiérrez-Galán & Alonso (2016)
Ziziphus spina-christi	Rhamnaceaea	Wild			●	Dunn et al. (2018)

SUPPLEMENTARY MATERIAL

Table SI. Relative importance of the 40 environmental predictors of the eight Species Distribution Models for *Streptopelia turtur* in the second European Breeding Bird Atlas, EBBA2 (Keller *et al.* 2020) and their weighted Ensemble Prediction. Variable importance ranges between 0 (no importance) to 100 %.

Name of variable (weighted ensemble prediction of 8 SDMs)	**Variable importance %**	**Type of variable**
Latitude	32.5	abiotic
Mean temperature in the breeding period	24	abiotic
Rainfed cropland	5.9	biotic
Mean annual temperature	5.5	abiotic
Evapotranspiration in the breeding period	5.1	abiotic
Minimum temperature of the coldest month	4.7	abiotic
Maximum temperature of the warmest month	2.6	abiotic
Longitude	2.4	abiotic
Well developed soils	1.9	biotic
Mean elevation	1.8	abiotic
Total annual precipitation	1.6	abiotic
Wood biomass	1.6	biotic
Total precipitation in the breeding period	1.1	abiotic
Mean slope	1.1	abiotic
Broadleaved forests	1.1	biotic
Human population density	1	abiotic
Urban areas	0.8	abiotic
Rainfed tree crops	0.6	biotic
Accumulated NDVI in the breeding period	0.5	biotic
Distance to the coastline	0.5	abiotic
Grassland	0.5	biotic
Mosaic natural vegetation	0.5	biotic
Shannon habitat diversity Index	0.5	biotic
Irrigated crops	0.3	biotic
Average forest canopy height	0.3	biotic
Young soils – weakly developed	0.3	abiotic
Coniferous forests	0.2	biotic
Bare areas	0.2	biotic
Mixed broadleaved and coniferous forests	0.2	biotic
Mosaic cropland – natural vegetation	0.2	biotic
Well developed and acid soils	0.2	abiotic
Wet soils	0.2	abiotic
Soils rich in clay	0.2	abiotic
Shannon soil diversity Index	0.2	biotic
Wetlands	0	biotic
Permanent ice	0	abiotic
Shrubland	0	biotic

Sparse vegetation	0	biotic
Continental water bodies	0	abiotic
Saline soils	0	abiotic