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ORIGINAL PAPER

The occurrence of cavities in fruit trees: effects of tree age and management on biodiversity in traditional European orchards

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Abstract The formation of tree-cavities is an important ecological factor since many animals in woody habitats are cavity users. Recent research focuses on tree-cavity formation and the associated cavity networks in forest ecosystems. However, although traditional European orchards are important habitats for secondary cavity users, ecological research on the factors associated with the occurrence of cavities in fruit trees is widely missing. In particular, fruit tree pruning management may affect decay-cavity formation due to the pruning wounds allowing heart rot and decay to enter the tree. Here, we present a cross-sectional study investigating 608 fruit trees in 30 study plots of three European fruit-growing regions to identify factors associated with decay-cavity occurrence in fruit trees. Presence of decay-cavities was positively related to trunk diameter. Moreover, fruit trees of low vitality and with woodpecker-cavities featured more often decay-cavities than trees of high vitality or without woodpecker-cavities. Apple trees featured higher numbers of cavities at younger age than other fruit trees. Occurrence of decay-cavities was also related to the past removal of large main branches. Accordingly, traditional orchards are cavity-rich habitats if they comprise high proportion of old fruit trees, in particular apple trees, and if pruning management produces large pruning wounds. Thus, differential tree pruning and fruit-growing traditions across Europe result in different cavity densities in traditional orchards. Preservation of existing and potential cavity trees and selective removal of large branches from apple trees are recommended as conservation measures establishing high cavity densities and increasing the associated biodiversity in the agricultural landscape.

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Introduction

The formation of tree-cavities is a key factor for animal communities living in habitats containing trees. The continuing formation process provides constant renewal of an essential resource for cavity-nesting and cavity-roosting vertebrates (e.g. Martin et al. 2004) and creates the habitat for a specialized arthropod community (Grove 2002). Woodpeckers actively build their own cavities (excavators, Cockle et al. 2011). However, many cavity users are non-excavators, usually characterized as secondary cavity users. They depend on existing cavities, created by excavators or by fungal heart rot and decay. It is well known that availability of tree-cavities limits population size of secondary cavity users (Cockle et al. 2010; Newton 1994; 1998). Populations of keystone cavity excavators therefore can affect whole populations and communities of cavity users (Blanc and Walters 2008a; Martin et al. 2004). Only recently, studies in different types of forests around the world showed that decay-cavities are of crucial importance for tree-cavity networks, in particular for larger vertebrates such as non-passerine birds (Blanc and Walters 2008b; Cockle et al. 2011, 2012; Koch et al. 2008a; Remm and Lohmus 2011).

Traditional high trunk orchards (tall fruit trees dispersed on cropland, meadows or pastures, trunk height >1.60 m; Herzog 1998) represent semi-natural habitats of high biodiversity with specialised communities occurring within intensified agricultural landscapes in many European countries (e.g. Herzog 1998; Barker et al. 2011; Knaus et al. 2011; Table 1). The intensification of agricultural production resulted in the loss of many traditional orchards and the associated biodiversity (Donald et al. 2001, 2006) due to the installation of modern cultivation systems. Although the preservation and creation of natural tree-cavities is often mentioned as a key measure in action plans of the conservation of orchard fauna, ecological research on the factors affecting occurrence and formation of cavities in fruit trees is widely missing.

Investigation of pruning effects on sapwood discoloration, heart rot and wood decay has a long-lasting history in forestry, because timber production is directly affected by pruning wounds resulting from management actions (Deflorio et al. 2007; Dujesiefken et al. 2005; O'Hara 2007; Seifert et al. 2010). Decay at pruning wounds of forest trees depends on the time for the occlusion reaction by the tree and thus, on the size of pruning wounds. Depending on tree species pruning wounds of 5–10 cm diameter often do not lead to discoloration and decay (Dujesiefken and Stobbe 2002). Wounds with larger diameters are exposed to the environment so long that they represent entrances for decay fungi (Schwarze et al. 2000). It is therefore likely that the traditional pruning management actions in orchards not only affect fruit yield but also inoculation of heart rot and formation of decay-cavities. Differences in the techniques and traditions of fruit tree pruning and in the composition of fruit tree species might therefore be important for the cavity formation processes in traditional high trunk orchards.

The aim of this study was to investigate the occurrence of decay-cavities in relation to trunk diameter, tree vitality, and pruning characteristics of fruit trees. Including three regions in Western Europe with different fruit-growing traditions ensured a high variability of pruning treatments. We expected that the occurrence of decay-cavities is positively

Table 1 Secondary cavity users (vertebrates) in traditional orchards of European temperate zone

Species	Breeding	Roosting
Birds		
Athene noctua	×	×
Certhia brachydactyla	×	×
Certhia familiaris	×	×
Columba oenas	×	×
Cyanistes caeruleus	×	×
Ficedula hypoleuca	×	×
Ficedula albicollis	×	×
Jynx torquilla	×	×
Otus scops	×	×
Parus major	×	×
Passer montanus	×	×
Periparus ater	×	×
Phoenicurus phoenicurus	×	×
Poecile palustris	×	×
Poecile montanus	×	×
Sitta europaea	×	×
Sturnus vulgaris	×	×
Upupa epops	×	×
Mammals		
Dryomys nitedula	×	×
Eliomys quercinus	×	×
Glis glis	×	×
Martes martes	×	×
Muscardinus avellanarius	×	×
Mustella nivalis		×
Myotis mystacinus		×
Myotis nattereri		×
Myotis bechsteinii	×	×
Myotis daubentonii	×	×
Nyctalus leisleri		×
Nyctalus noctula		×
Nyctalus lasiopterus		×
Plecotus auritus	×	×
Sciurus vulgaris	×	×

related to pruning characteristics such as the removal of large structural branches (i.e. primary main branches radiating from the trunk of a fruit tree, in arboricultural terminology called scaffold branches) or the number of pruning cuts, while controlling for the positive effects of trunk diameter and the negative effects of measures of low tree vitality on cavity occurrence. The results give insights into the mechanisms of cavity formation in traditional orchards and might be applied to accelerate cavity formation rate and to increase density of cavities in orchards.

Materials and methods

Study plots

For the detailed recording of tree characteristics and their pruning treatments, we selected 30 study plots in stands of standard fruit trees, located in three fruit-growing regions of Switzerland (Cantons Basel-Landschaft, Schaffhausen/Thurgau) and Germany (County of Ludwigsburg, Baden-Württemberg). The three regions allowed for a sufficient sample of different fruit tree species and for a high variation of tree pruning treatments in the data. Within the regions, study plots were selected in the context of a current research project on the little owl (*Athene noctua*, Bock et al. 2013). The study plots were placed at potential little owl home-ranges represented by the presence of an artificial nest box provided by expert ornithologists. In each stand, the artificial nest box was the reference point for the assessments, and we recorded the characteristics of the 25 trees nearest to the nest box. Non-fruit trees were eliminated from the data set. This selection of trees provided a balanced sample of different fruit tree species of all ages, in particular including old fruit trees. However, it is not a representative sample of orchards in the study regions.

Tree characteristics and cavities

In May to July 2011, for each standard fruit tree (i.e. fruit tree with high trunk) in the study plots, we recorded the fruit tree species (apple tree *Malus domestica*; pear tree *Pyrus communis*; plum tree *Prunus domestica*; cherry tree *Prunus avium*) and the trunk diameter at breast height (dbh). Moreover, vitality was assessed as the estimated proportion of dead wood in the crown defining six categories (5 = 0–10 %, 4 = 10–30 % dead wood; 3 = 30–50 % dead wood; 2 = 50–70 % dead wood; 1 = 70–90 % dead wood; 0 = 90–100 %). This was considered to be a visual measure of the health status of the tree. Two measures of tree pruning treatments were recorded by using binoculars to see details in the crown of the tree. First, the total number of pruning cuts with cut surface diameters >4 cm was counted, irrespective of the age of the pruning cuts or whether the cut surface was healed-over by callus formation or not. Second, we counted the number of removed main structural branches (scaffold branches; branch diameter > half the trunk diameter dbh). Two kinds of cavities were recorded. First, the number of decay-cavities with an entrance of >6 cm diameter was counted from the ground by using binoculars. We counted only entrances with an estimated depth of >15 cm and omitted initial cavities without a discernible extension into the tree heart. Second, we recorded whether or not the focal tree featured woodpecker-cavities. Here, cavity entrances of all diameters were included. Woodpecker-cavities were produced by great spotted woodpecker (*Dendrocopos major*), lesser spotted woodpecker (*Dendrocopos minor*) or green woodpecker (*Picus viridis*). We used the occurrence of woodpecker-cavities as a proxy for the condition of the heart wood of trees (heart rot due to fungal decay) and thus as an indirect measure of fungal infection (Jackson and Jackson 2004; Pasinelli 2007; Zahner et al. 2012).

Statistical analyses

We used generalized linear mixed models (GLMM) fit by the Laplace approximation to analyse the relationships between tree characteristics and trunk diameter (dbh) and to examine the factors associated with cavity occurrence and cavity numbers. Models were fit in the program R (R Development Core Team 2012) using the functions glmer from the library lme4 (Bates 2005). To account for the dependency of the observations from the same plot the factor *study plot* was included in all models as a random effect. Since data on the numbers of decay-cavities were zero-inflated, we used a two-step analysis. First, we used GLMM with binomial error distribution and logit-link function to analyse factors associated with the presence of decay-cavities (Bolker et al. 2008). Second, we investigated the factors associated with the number of decay-cavities conditional on the presence of decay-cavities. Here, Poisson error distribution was assumed and the log-link function used. For the analyses of the number of decay-cavities we restricted the data to apple and cherry trees because of insufficient sample sizes for plum and pear trees with more than one cavity. For both analyses, a first full model was built incorporating all main effects of tree characteristics (trunk diameter, tree species, vitality, number of woodpecker-cavities), of tree pruning treatments (number of pruning cuts, number of removed main branches), all two-way interactions between trunk diameter and the other predictors, and a second order polynomial for trunk diameter. Non-significant interactions and a non-significant second order polynomial were step-wise omitted from the models, but no further model selection was performed, i.e. all main effects remained in the final models.

Credible intervals (95 % CrI) for the model parameter estimates were calculated as the 2.5 and 97.5 % quantiles of 1,000 random values sampled from the joint posterior distribution of the model parameters using the function sim() from library "arm" (Gelman and Hill 2007). CrI served to evaluate significance of parameters. Predictions and their 95 % CrI were obtained from the same sample of 1,000 random values from the joint posterior distribution of the model parameters.

Results

In total, we recorded cavity presence, cavity numbers, tree characteristics and tree pruning treatments of 608 fruit trees within 30 study plots (apple trees: $n = 326$, 53.62 %; pear trees: $n = 56$, 9.21 %; plum trees: $n = 59$, 9.70 %; cherry trees: $n = 167$, 27.47 %).

Differences in vitality and pruning treatments between tree species

The vitality of the trees decreased significantly with dbh, i.e. with age, and levelled off in trees of large dbh. Pear trees showed significantly higher vitality than the other fruit tree species which showed no between-species differences in vitality (Table 2; Fig. 1).

We found woodpecker-cavities in 17.1 % of the fruit trees (in 20.9 % of apple trees; in 17.9 % of pear trees; in 13.6 % of plum trees; in 9.6 % of cherry trees). Woodpecker-cavity presence increased with dbh of trees and was significantly lower in cherry trees compared to other fruit tree species (Table 2; Fig. 1). Also, pear trees tended to have lower woodpecker-cavity presence than apple trees. The number of removed main branches increased with dbh of trees. However, fruit tree species differed significantly in the number of removed main branches, with significant lower branch removal in cherry trees than in other tree species (Table 2; Fig. 1). The number of pruning cuts was significantly higher in apple trees than in other fruit tree species of the same size. When including region post hoc into the models, we found higher numbers of removed main branches in Germany than in Switzerland ($p < 0.01$), but no differences between regions in the number of pruning cuts ($p = 0.19$). Vitality tended to be lower in Germany ($p = 0.05$), but there was no difference in the woodpecker-cavity presence between regions ($p = 0.09$).

Table 2 Relationships between trunk diameter and other tree characteristics in the four fruit tree species

Parameter	Categories	Vitality			Woodpecker-cavities		
		$\widehat{\beta}$	95 % CrI lwr	95 % CrI upr	$\widehat{\beta}$	95 % CrI lwr	95 % CrI upr
Intercept		3.50	3.33	3.68	−1.47	−1.89	−1.06
Trunk diameter		**−0.53**	−0.64	−0.43	**0.73**	0.47	1.01
Trunk diameter^2		**0.12**	0.05	0.19	–	–	–
Tree species	Apple tree	0			0		
	Pear tree	**0.41**	0.09	0.73	−0.67	−1.53	0.20
	Plum tree	0.02	−0.31	0.36	0.02	−0.84	0.87
	Cherry tree	0.15	−0.10	0.39	**−1.24**	−1.99	−0.49
Parameter	**Categories**	**Pruning cuts**			**Removed main branches**		
		$\widehat{\beta}$	95 % CrI lwr	95 % CrI upr	$\widehat{\beta}$	95 % CrI lwr	95 % CrI upr
Intercept		1.72	1.58	1.87	−0.58	−0.84	−0.34
Trunk diameter		**0.92**	0.86	0.99	**0.76**	0.58	0.94
Trunk diameter^2		**−0.27**	−0.30	−0.23	**−0.19**	−0.29	−0.09
Tree species	Apple tree	0			0		
	Pear tree	**−0.35**	−0.50	−0.20	−0.04	−0.40	0.30
	Plum tree	−0.13	−0.32	0.06	−0.07	−0.56	0.46
	Cherry tree	**−0.48**	−0.60	−0.35	**−0.82**	−1.22	−0.43

Significant parameter estimates are shown in bold. Apple tree was used as reference species for the species comparisons. $N = 608$ trees

Between study plots: vitality: variance = 0.091; woodpecker-cavities: variance = 0.494; pruning cuts: variance = 0.138; removed main branches: variance = 0.288

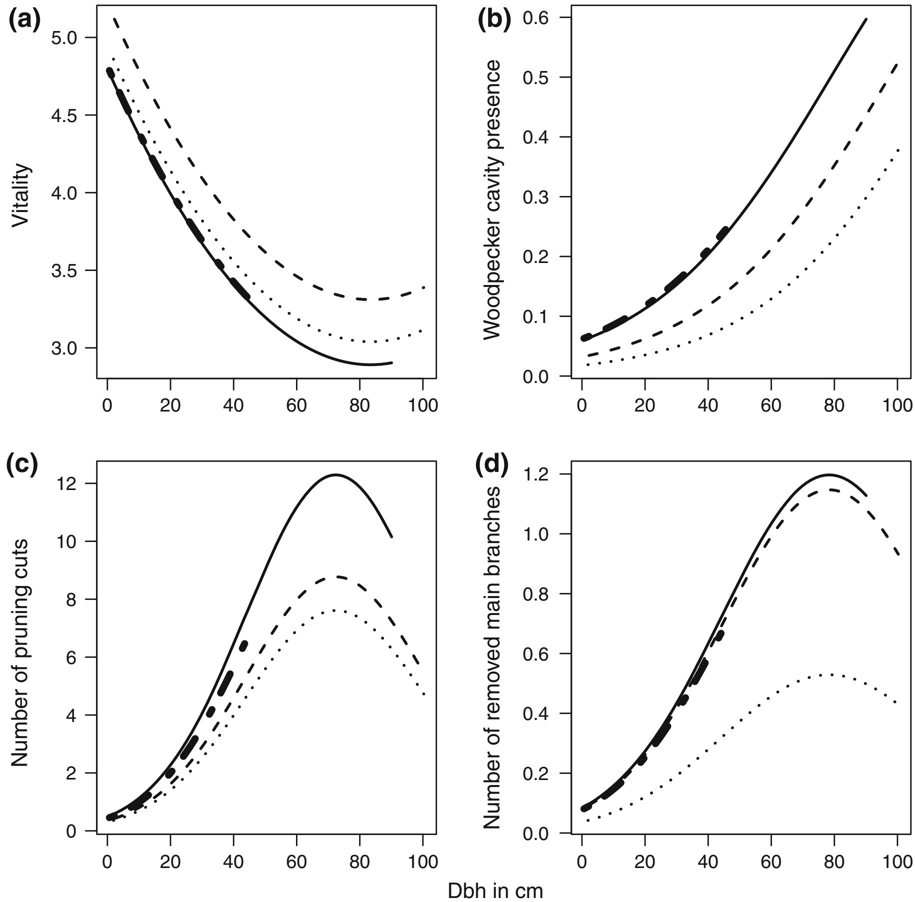

Fig. 1 The relationships between trunk diameter (dbh) and **a** tree vitality (classified proportion of dead wood in the crown; 5 = 0–10 % dead wood, 0 = 90–100 % dead wood), **b** woodpecker-cavity presence, **c** number of pruning cuts, and **d** number of removed main branches for apple trees (*solid line*; $n = 326$), pear trees (*broken line*; $n = 56$), plum trees (*short line*; $n = 59$), and cherry trees (*dotted line*; $n = 167$)

Decay-cavities

We found large decay-cavities in 17.1 % of the totally 608 fruit trees (in 20.9 % of apple trees; in 10.7 % of pear trees; in 8.5 % of plum trees; in 13.7 % of cherry trees). Presence of decay-cavities was positively related to dbh. This relationship was better described by a second order polynomial than by a linear relationship (Table 3). The other main factor associated with the presence of decay-cavities was the presence of woodpecker-cavities, which we used as a proxy for the fungal decay of the heart wood. Trees with woodpecker-cavities showed significantly increased probability to contain decay-cavities compared to trees without woodpecker-cavities (Table 3; Fig. 2). Furthermore, trees of low vitality showed a higher presence of decay-cavities than trees of high vitality (Table 3; Fig. 2). One of the two pruning characteristics showed a significant effect on the presence of decay-cavities: the number of removed main branches was positively associated with the presence of decay-cavities (Table 3; Fig. 3). Tree species differed in decay-cavity

Table 3 Factors associated with the presence of decay-cavities

Parameter	Categories	$\hat{\beta}$	95 % CrI lwr	95 % CrI upr
Intercept		−2.08	−3.08	−1.06
Trunk diameter		**1.64**	0.92	2.33
Trunk diameter^2		**−0.38**	−0.65	−0.09
Tree species	Apple tree	0		
	Pear tree	**−1.81**	−3.05	−0.62
	Plum tree	0.77	−0.56	2.08
	Cherry tree	−0.17	−1.10	0.70
Vitality		**−0.22**	−0.44	−0.002
Woodpecker-cavities		**1.77**	1.11	2.39
Nr. pruning cuts		0.004	−0.07	0.07
Nr. removed main branches		**0.70**	0.40	1.01

Significant parameters estimates are shown in bold. Apple tree was used as reference species for the species comparisons. $N = 608$ trees

Between study plot variance = 0.826

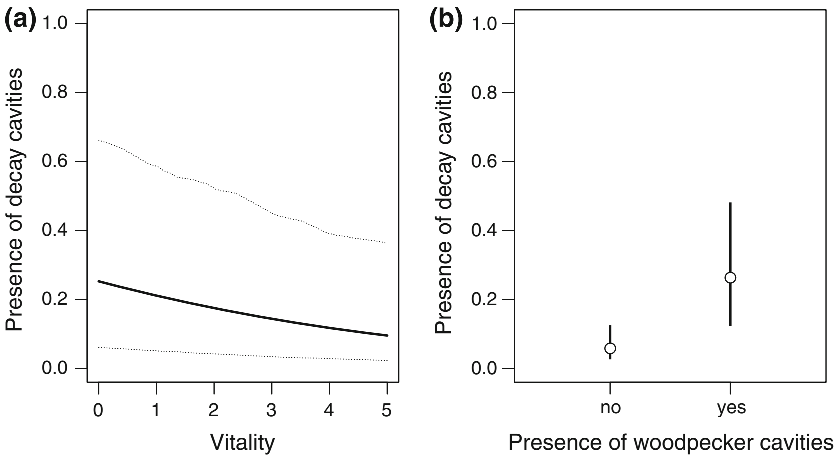

Fig. 2 Presence of decay-cavities (model estimates and 95 % CrI) in relation to vitality measures. **a** Tree vitality (classified proportion of dead wood in the crown; 5 = 0–10 % dead wood, 0 = 90–100 % dead wood), **b** presence of woodpecker-cavities. $N = 608$ trees

presence. In particular, pear trees featured less often decay-cavities than other fruit tree species (Table 3). Figure 4 shows the predicted decay-cavity presence in fruit trees as encountered in the study plots, i.e. it takes into account the differences in tree characteristics and pruning actions between tree species. Decay-cavity presence was highest in apple trees, followed by pear trees and was lowest in cherry trees of the same size (Fig. 4). This resulted primarily from the steep decrease of vitality (including an increase in woodpecker-cavity presence) and the frequent removal of main branches in apple trees. Decay-cavity presence in plum trees was similar to apple trees, but since plum trees reached only limited trunk diameters, cavity presence remained at low levels. Regions showed no differences in decay-cavity presence when controlling for tree and pruning characteristics ($p = 0.1$), but

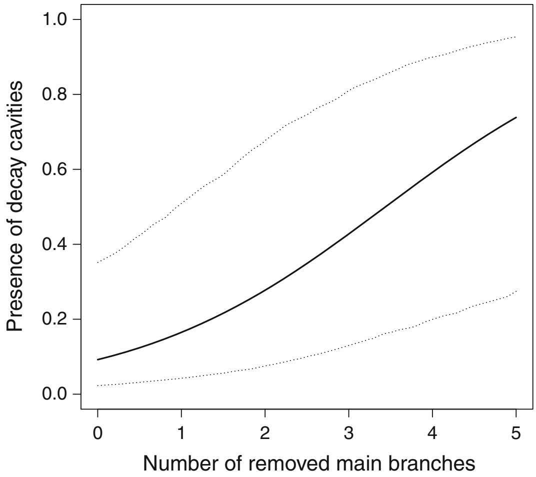

Fig. 3 Presence of decay-cavities (model estimates and 95 % CrI) in relation to the number of removed main branches (scaffold branches) of a fruit tree. $N = 608$ trees

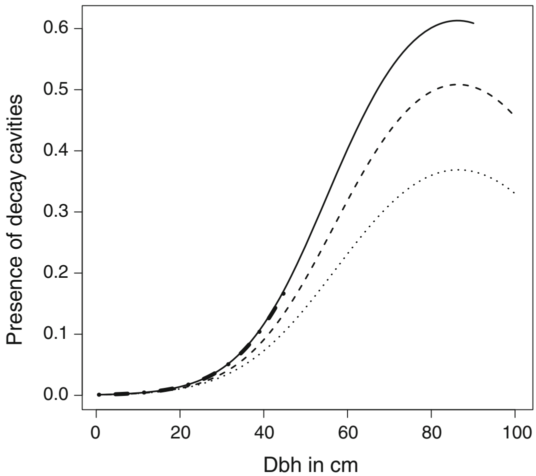

Fig. 4 Presence of decay-cavities (model estimates) for apple trees (*solid line*; $n = 326$), pear trees (*broken line*; $n = 56$), plum trees (*short line*; n = 59), and cherry trees (*dotted line*; n = 167) in relation to trunk diameter (dbh) when considering between-species differences in vitality measures and pruning treatments (see Fig. 1)

decay-cavity presence was higher in Germany than in Switzerland due to more frequent removal of main branches and the low tree vitality in Germany.

The number of decay-cavities in trees with at least one decay-cavity increased with dbh (i.e. with age; Table 4). Trees with woodpecker-cavities showed not only higher probability for decay-cavity presence, but they also featured more decay-cavities than trees without woodpecker-cavities (Table 4). Moreover, the number of decay-cavities tended to be positively related to the number of removed main branches. When controlling for these effects, the number of decay-cavities showed no differences between apple and cherry trees. However, since apple trees showed higher presence of woodpecker-cavities and more removed main branches, the number of decay-cavities was significantly higher in apple than in cherry trees.

Discussion

In our study, 17 % of fruit trees featured decay-cavities. Thus, as compared with managed forest ecosystems where density of decay-cavity trees is often below 8 % (e.g. Bennet et al.

Table 4 Factors associated with the number of decay-cavities in trees with at least one decay-cavity

Parameter	Categories	$\widehat{\beta}$	95 % CrI lwr	95 % CrI upr
Intercept		0.69	0.19	1.15
Trunk diameter		**0.15**	0.01	0.28
Tree species	Apple tree	0		
	Cherry tree	−0.19	−0.58	0.22
Vitality		−0.03	−0.13	0.07
Woodpecker-cavities		**0.35**	0.10	0.61
Nr. pruning cuts		−0.00	−0.04	0.03
Nr. removed main branches		0.10	−0.01	0.20

Significant parameters estimates are shown in bold. Apple tree was used as reference species for the species comparisons. $N = 91$ trees

Between study plot variance = 0.00; $n = 68$ apple trees; 23 cherry trees

1994; Cockle et al. 2010, 2011; Martin et al. 2004), managed orchards seem to be a cavity rich habitat. However, the selected plots were included because they were classified as ecologically valuable plots by ornithologist experts. Therefore, this study represents the situation in orchards at the high value end rather than the state of orchards of the study areas in general. There is no evidence that tree pruning or vitality differed from orchards of lower ecological quality and even if this would be the case, it is not expected that the relationships between tree characteristics and presence of decay-cavities differ from other orchards. We suggest that the main difference between the selected high quality plots and other orchard habitats was the mean age of the trees. The presence of cavities in these high quality orchards allowed a cross-sectional study to identify factors associated with cavity formation in fruit trees. The positive association between trunk diameter and cavity presence, and the negative relationship between vitality and cavity presence are well known from forestry (Gibbons et al. 2000; Koch et al. 2008b; Remm et al. 2006; Robles et al. 2011), but have been only sporadically investigated in trees of the agricultural landscape. Our results confirm that cavity presence increases with trunk diameter and is high at reduced vitality also in fruit trees. Trunk diameter as well as vitality in terms of dead wood in the crown are traits strongly related to the probability that fungal decay and heart rot enter the tree. Thus, presence of decaying fungi in the heart of the tree is most probably the fundamental factor affecting cavity formation. Also the presence of woodpecker-cavities indicates occurrence of invisible heart rot in fruit trees (Pasinelli 2007; Zahner et al. 2012). The woodpeckers' preference for infested trunk parts suggests that both types of cavities independently are related to the presence of heart rot. However, with our data we cannot exclude a direct causal effect of woodpecker-cavities on decay-cavity formation.

Tree species in forests around the world show differences in the susceptibility to cavity formation (e.g. Remm et al. 2006). In our study area in European orchards of the temperate zone, apple trees held most woodpecker-cavities and showed the lowest levels of vitality compared to other fruit tree species. This suggests that apple trees are particularly prone to heart rot resulting in higher rates of decay-cavity formation and higher attractiveness to woodpeckers. In contrast, cherry trees showed significantly reduced woodpecker-cavity presence representing low heart rot infestation in relation to other fruit tree species. One of six apple trees, but only one of twenty cherry trees of 30 cm dbh featured woodpecker-cavities. Thus, apple trees provide both types of tree-cavities at a younger age than the other fruit tree species.

The primary main branches radiating from the trunk of a fruit tree (i.e. the scaffold branches) are the most important structure of traditional high-stem fruit trees. That fruit trees achieve their optimal form is the key issue of early fruit tree care treatments. It ensures high productivity and tree health due to the reshaping of the tree (Coombs et al. 2001). Dead or broken scaffold branches are regularly removed, leaving large pruning wounds at the trunk. Since cost effectiveness of traditional fruit production on high-stem trees decreased in the past decades, scaffold branches were increasingly removed to ensure an effective management of grasslands, arable fields or gardens below the trees. Our study provides strong evidence that removing scaffold branches enhances the formation of large decay-cavities in the tree trunk. More than half of the trees where all scaffold branches had been removed showed decay-cavities at their trunk. The large pruning wounds provide entrance to wood-decay fungi into the heart of the tree before the wound occlusion by the tree is finished (Adaskaveg et al. 1993; Ogawa and English 1991; Seifert et al. 2010). These results suggest also that removal of large branches above the scaffold branches promotes decay-cavity formation.

Since the middle of the last century, creation of one radiation of few scaffold branches, known as the Oeschberg or the Swiss method of pruning (Spreng 1944), came up in some regions in Europe, replacing tree formation creating several super-imposed radiations of main branches. The method resulted in preventing large pruning wounds, because in such trees the removal of scaffold branches represents an unreasonably large reduction of the tree and strongly reduces productivity. These pruning traditions vary between countries and regions within Europe and also at a small spatial scale, tree owners differ in pruning treatments and fruit tree care. Therefore, it is likely that the number of removed main branches creating large pruning wounds, and thus the number of decay-cavities, differs at all spatial scales, from the local scale within orchards of different tree owners to the large scale across Europe.

Past studies investigating the availability of tree-cavities in European orchards showed that abandoned orchards without regular tree care featured ten times more cavities than orchards with regular tree care (Bitz 1992). However, we do not know whether tree care decelerates cavity formation by physiological reactions of the tree and by the new structural characteristics of the crown, or whether regular tree care eliminates branches or whole trees with cavities. Since there is evidence that stub occlusion is positively affected by the growth rate of the tree (Seifert et al. 2010) and pruning treatment affects the growth of fruit trees (Coombs et al. 2001) we suggest that both mechanisms might be involved.

Conclusions

Due to the importance to a large community of cavity using organisms, traditional orchards are a key habitat in European agricultural landscapes (Herzog 1998; Table 1). In many European countries, subsidies and management recommendations exist to prevent this habitat from further loss. Moreover, single large fruit trees featuring cavities represent important ecological structures in European agricultural landscapes. In the last decades conservation focused on replantation of fruit trees, on preservation of old standard trees with large trunk diameter and on the research on and the application of optimal management of grasslands and fields below fruit trees (Coudrain et al. 2010; Martinez et al. 2010; Mermod et al. 2009; Weisshaupt et al. 2011). However, studies in traditional orchards show that the lack of suitable nest sites severely limits density of secondary cavity nesters (Coudrain et al. 2010; Van Nieuwenhuyse et al. 2008). Moreover, recent studies show that tree-cavities are important winter roost-sites for vertebrates, also in orchards (Bock et al. 2013; Grüebler et al. 2013; Paclík and Weidinger 2007). Nevertheless, conservation of natural cavities remains a neglected issue in the conservation of agricultural habitats. Our results show that presence and number of natural cavities in standard fruit trees is associated with the age of the tree, the tree species, tree vitality and the pruning management of the trees. Accordingly, the availability of tree-cavities in traditional orchards and in agricultural landscapes containing large fruit trees depends on the composition of tree age and species and on the past management. As shown for forest systems worldwide (Edworthy et al. 2012; Lindenmayer et al. 2012a, b), we suggest that old and decaying fruit trees featuring cavities in agricultural landscapes show high mortality and low recruitment rates due to changes in the agricultural management. Thus, in addition to the claim for new plantations and creation of standard fruit trees to replace disappearing resources, we strongly recommend conserving decaying fruit trees and trees with cavities from removal as long as possible. Moreover, also fruit tree branches featuring cavities should persist. Apple trees often feature cavities already at small trunk diameters. Such trees are likely to be important in orchards with many young trees. Thus, new plantations should include a high proportion of apple trees. In forestry, different methods to promote cavity formation in trees have been proposed (e.g. Filip et al. 2004). We suggest that removing large branches from fruit trees (in particular in apple trees) promotes cavity formation and may be used as a conservation pruning action to increase cavity numbers throughout the agricultural landscape. However, this is still a long-term measure because the formation process of decay-cavities needs many years.

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References

Adaskaveg JE, Miller RW, Gilbertson RL (1993) Wood decay, lignicolous fungi, and decline of peach trees in South Carolina. Plant Dis 77:707–711

Barker S, Burrough AE, Cordrey L, Merry K, Wedge C (2011) Conserving the wildlife of traditional orchards. Br Wildl 23:8–16

Bates D (2005) Fitting linear mixed models in R—using lme4 package. R News 5:27–30

Bennet AF, Lumsden LF, Nicholls AO (1994) Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. Pac Conserv Biol 1:222–235

Bitz A (1992) Avifaunistische Untersuchungen zur Bedeutung der Streuobstwiesen in Rheinland-Pfalz. Beiträge Landespflege Rheinland-Pfalz 15:593–719

Blanc LA, Walters JR (2008a) Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. Ecology 89:506–514

Blanc LA, Walters JR (2008b) Cavity-nest webs in a longleaf pine ecosystem. Condor 110:80–92

Bock A, Naef-Daenzer B, Keil H, Korner-Nievergelt F, Perrig M, Grüebler MU (2013) Roost-site selection of little owls in relation to environment and life-history stages. Ibis 155:847–856

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Cockle KL, Martin K, Drever MC (2010) Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol Conserv 143:2851–2857

Cockle KL, Martin K, Wesolowski T (2011) Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front Ecol Environ 9:377–382

Cockle KL, Martin K, Robledo G (2012) Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. For Ecol Manag 264:210–219

Coombs D, Blackburne-Maze P, Cracknell M (2001) The complete book of pruning. Cassell Paperbacks, London

Coudrain V, Arlettaz R, Schaub M (2010) Food or nesting place? Identifying factors limiting Wryneck populations. J Ornithol 151:867–880

Deflorio G, Barry KM, Johnson C, Mohammed CL (2007) The influence of wound location on decay extent in plantation-grown *Eucalyptus globulus* and *Eucalyptus nitens*. For Ecol Manag 242:353–362

Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc B 268:25–29

Donald PF, Sanderson FJ, Burfield IJ, Bommel FPJ (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agric Ecosyst Environ 116:189–196

Dujesiefken D, Stobbe H (2002) The Hamburg tree pruning system—a framework for pruning of individual trees. Urban For Urban Green 1:75–82

Dujesiefken D, Liese W, Shortle W, Minocha R (2005) Response of beech and oaks to wounds made at different times of the year. Eur J For Res 124:113–117

Edworthy AB, Wiebe KL, Martin K (2012) Survival analysis of a critical resource for cavity-nesting communities: patterns and tree cavity longevity. Ecol Appl 22:1733–1742

Filip GM, Parks CG, Baker FA, Daniels SE (2004) Artificial inoculation of decay fungi into Douglas-fir with rifle or shotgun to produce wildlife trees in western Oregon. West J Appl For 19:211–215

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge

Gibbons P, Lindenmayer DB, Barry SC, Tanton MT (2000) Hollow formation in eucalypts from temperate forests in southeastern Australia. Pac Conserv Biol 6:218–228

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Grüebler MU, Widmer S, Korner-Nievergelt F, Naef-Daenzer B (2013) Temperature characteristics of winter roost sites for birds and mammals: tree cavities and anthropogenic alternatives. Int J Biometeorol. doi:10.1007/s00484-013-0643-1

Herzog F (1998) Streuobst: a traditional agroforestry system as a model for agroforestry development in temperate Europe. Agrofor Syst 42:61–80

Jackson AJ, Jackson BJ (2004) Ecological relationships between fungi and woodpecker cavity sites. Condor 106:37–49

Knaus P, Graf R, Guélat J, Keller V, Schmid H, Zbinden N (2011) Historischer Brutvogelatlas. Die Verbreitung der Schweizer Brutvögel seit 1950. Schweizerische Vogelwarte, Sempach

Koch AJ, Munks SA, Driscoll D, Kirkpatrick JB (2008a) Does hollow occurrence vary with forest type? A case study in wet and dry *Eucalyptus obliqua* forest. For Ecol Manag 255:3938–3951

Koch AJ, Munks SA, Woehler EJ (2008b) Hollow-using vertebrate fauna of Tasmania: distribution, hollow requirements and conservation status. Aust J Zool 56:323–349

Lindenmayer DB, Blanchard W, McBurney L, Blair D, Banks S, Likens GE, Franklin JF, Laurance WF, Stein JAR, Gibbons P (2012a) Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. PLoS One 7:e41864

Lindenmayer DB, Laurance WF, Franklin JF (2012b) Global decline in large old trees. Science 338:1305–1306

Martin K, Aitken KEH, Wiebe KL (2004) Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106:5–19

Martinez N, Jenni L, Wyss E, Zbinden N (2010) Habitat structure versus food abundance: the importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. J Ornithol 151:297–307

Mermod M, Reichlin TS, Arlettaz R, Schaub M (2009) The importance of ant-rich habitats for the persistence of the Wryneck *Jynx torquilla* on farmland. Ibis 151:731–742

Newton I (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol Conserv 70:265–276

Newton I (1998) Population limitation in bird. Academic Press, San Diego

O'Hara KL (2007) Pruning wounds and occlusion: a long-standing conundrum in forestry. J For 105:131–138

Ogawa JM, English H (1991) Diseases of temperate zone tree fruit and nut crops. University of California, Oakland

Paclík M, Weidinger K (2007) Microclimate of tree cavities during winter nights—implications for roost site selection in birds. Int J Biometeorol 51:287–293

Pasinelli G (2007) Nest site selection in middle and great spotted woodpeckers *Dendrocopos medius* & *D. major*: implications for forest management and conservation. Biodivers Conserv 16:1283–1298

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Remm J, Lohmus A (2011) Tree cavities in forests—the broad distribution pattern of a keystone structure for biodiversity. For Ecol Manag 262:579–585

Remm J, Lohmus A, Remm K (2006) Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines. For Ecol Manag 221:267–277

Robles H, Ciudad C, Matthysen E (2011) Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. For Ecol Manag 261:1428–1435

Schwarze FWMR, Engels J, Mattheck C (2000) Fungal strategies of wood decay in trees. Springer, Berlin

Seifert T, Nickel M, Pretzsch H (2010) Analysing the long-term effects of artificial pruning of wild cherry by computer tomography. Trees 24:797–808

Spreng H (1944) Neuzeitliche Kronenpflege der Obstbäume. Verbandsdruckerei AG Berne, Oeschberg

Van Nieuwenhuyse D, Génot J-C, Johnson DH (2008) The little owl. Conservation, ecology and behavior of *Athene noctua*. Cambridge University Press, Cambridge

Weisshaupt N, Arlettaz R, Reichlin TS, Tagmann-Ioset A, Schaub M (2011) Habitat selection by foraging Wrynecks *Jynx torquilla* during the breeding season: identifying the optimal habitat profile. Bird Study 58:111–119

Zahner V, Sikora L, Pasinelli G (2012) Heart rot as a key factor for cavity tree selection in the black woodpecker. For Ecol Manag 271:98–103