

Spatiotemporal variation in acorn production and damage in a Spanish holm oak (*Quercus ilex*) dehesa

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Abstract

Aim of study: There is a lack of knowledge about spatio-temporal patterns of acorn production in dehesas, especially regarding the influence of different agents causing acorn damage. We examined the spatial and temporal variability on acorn production and damage in four stands within a dehesa farm in 1997, 1998 and 1999.

Area of study: The study was carried out in a 1800 ha dehesa farm of Cáceres province, western Spain.

Material and methods: Acorns were sampled by means of seed traps placed in the canopy of six holm oak trees per stand. Acorns collected were counted and assessed for damage by *Curculio* weevils, *Cydia* moths and the bacterial pathogen *Brenneria quercina*.

Main results: Mean acorn production for the whole study period was 44.60 acorns m⁻², which did not vary significantly either among stands or among years. The variability among individual trees was very high (0-300 acorns m⁻²). The rate of infestation by *Curculio* was 7.64 ± 10.72%, by *Cydia* was 1.76 ± 3.33%, whereas 10.29 ± 16.12% of acorns were infested by *Brenneria*. We found no significant spatial differences, but the rates of acorn loss by insects varied among years. These rates were independent of annual acorn production and there was no correlation among damages by different pests, except between *Curculio* and *Cydia* in two crop years.

Research highlights: It can be concluded that acorn crops are synchronized at the within-farm level and that the temporal variation in acorn damages can be independent of crop size.

Key words: acorn production; *Brenneria*; *Curculio*; *Cydia*; dehesa; *Quercus ilex*; spatio-temporal variation.

Introduction

Dehesas are ecosystems consisting of low-density oak woodland with an understory composed of grasslands, shrublands, and croplands where livestock is extensively raised (San Miguel, 1994). The dehesa is the most widespread agroforestry land-use system in Europe (Moreno and Pulido, 2009) where it covers 3.1 million hectares in Spain and Portugal. Holm-oak (*Quercus ilex*) is the dominant tree species in this ecosystem, and it can be considered as an “ecosystem engineer” influencing many ecological processes (Jones *et al.*, 1994).

Holm oaks are small- to medium-sized trees that grow in poor substrates. Because of low stand density and tree pruning, dehesa trees greatly exceed forest trees in height and canopy area (Montero *et al.*, 2002). Holm oak is monoecious. Wind pollination occurs in

late April to early May, though fertilization and fruit set is delayed until late June. Fruit development proceeds until final size is reached in late September. Fruits may fall before maturity because of abortion, abnormal fruit development with sap exudation (“drippy” fruits) caused by *Brenneria quercina*, or insect infestation by borer larvae of moths (*Cydia* spp.: Tortricidae) and weevils (*Curculio elephas* Gyll.: Curculionidae).

In dehesas and other temperate oak-dominated systems acorns play a basic role in livestock and wildlife feeding. As a result of acorn predation by these animals, most forests and woodlands are threatened by lack of sexual regeneration (Gea-Izquierdo *et al.*, 2006). Despite this, our knowledge of acorn production patterns in space and time is still very limited, especially regarding the influence of different agents causing acorn damage in dehesas (Alejano *et al.*, 2012). Previous reports showed that production is highly variable, both between and within years and individuals (Álvarez *et al.*, 2002; Torres *et al.*, 2004; García-Mozo *et al.*, 2007),

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but there is a lack of studies analyzing spatial effects at local or regional scales.

The relationship between acorn production and site characteristics (climate and soil) has been widely reported in other oak species, showing that different sites can show great differences in acorn production at large geographical scales (Kelly and Sork, 2002; Abrahamson and Layne, 2003; Fearer *et al.*, 2008; Peter and Harrington, 2009). At regional scales Koenig *et al.* (1999) in North America reported synchrony of acorn production between individual trees. At lower scale, Díaz *et al.* (2009) in dehesas noted that holm-oak production was apparently not synchronized between populations separated by only a few tens of kilometers.

It has been reported that a strong inter-annual variability in seed production (*e.g.* mastings) may reduce seed predation by insects by the combined effect of satiating and starving seed consumers (Crawley and Long, 1995; Espelta *et al.*, 2008). Thus, annual fluctuation in acorn production can alter the dynamics of insect predators (Fukumoto and Kajimura, 2011). However, there is very little information on the variation of acorn damage between stands and years, which hampers decision making in relation to pest management.

In this paper we compared acorn production and damage in four stands within a dehesa farm in three consecutive years. Thus, we hypothesized that (i) as a consequence of edaphoclimatic and management variation, acorn production differs among stands within a farm; (ii) for a mast fruiting species, the spatial variation depends on the mast cycle, that is, the spatial pattern is not consistent among years; (iii) there are spatio-temporal differences in acorn infestation levels by different pre-dispersal agents; and (iv) the interaction of seeds and their predators is density-dependent as found in previous studies, probably fitting to an exponential function.

Material and methods

Study site

The study was carried out in a 1800 ha dehesa farm of Cáceres province, western Spain (San Blas, 39° 42' 9" N, 5° 55' 18" W). The site is located on a flat area at about 350 m asl. Holm-oaks grow scattered over a grassland matrix at an average density of 36 trees ha⁻¹ on oligotrophic, acid soils (pH 5.2). The climate is Mediterranean with dry and hot summers and cool and

rainy winters. Annual precipitation was 1180, 590 and 605 mm, and mean annual temperature was 18.9°C, 18.8°C and 18.6°C for 1997, 1998, and 1999, respectively. Based on our own records for the period 1965-2000, 1998 and 1999 were dry years whereas 1997 was the wettest year. All years sampled showed mean temperatures above the average value of the whole series (17.2°C).

Experimental design and collected data

Within the studied dehesa farm we established one study plot divided in four paddocks for management purposes. We randomly selected and marked a point inside each paddock and selected the six nearest adult trees (acorn-bearing individuals of at least 10 cm in stem diameter) from each site (24 trees in total) in October 1997. Tree density in these paddocks ranged from 22 to 66 trees ha⁻¹. The distance between plots ranged from 709 m to 3,200 m. Average size of trees was 7.48 ± 1.50 m (mean ± 1 SD) in height whereas the mean canopy radius was 3.97 ± 0.72, 4.73 ± 0.76, 3.56 ± 0.64 and 4.08 ± 0.57 m in the stands A, B, C and D, respectively. The pre-dispersal predation and cumulative production of mature acorns was monitored for these trees in October-January 1997-1998, 1998-1999, and 1999-2000 (hereafter, 1997, 1998, and 1999 acorn seasons).

Four seed traps were installed in each of the 24 trees. They consisted of 0.12 m² plastic buckets 25 cm in depth that were attached with wire to the lower canopy of trees in random positions. Traps operated from October 1997 to January 2000. Every January acorns accumulated into the traps in the previous autumn were collected and assigned *in situ* to one of the following categories: (1) sound acorns; (2) acorns infested by *Cydia* moths; (3) acorns infested by *Curculio* weevils, and (4) drippy fruits infested by *Brenneria*.

Tree fecundity or acorn production was estimated as the mean number of acorns m⁻². The incidence of each source of pre-dispersal damage was calculated as the number of acorns in a given category divided by the total number of acorns fallen in the traps.

Statistical analysis

The effects of year and stand on acorn production, sound acorns and damage were analyzed by means of General Linear Models (GLM) on a repeated-measured

ANOVA-type design with year as within-subject factor and trees as replicates (the same individual trees were sampled each year). Means were compared using Fisher's protected least significant difference (LSD) test at $p \leq 0.05$. Rates of pre-dispersal damage were arcsine-transformed. Relationships between different types of damages and their relationship with acorn crop size were evaluated by means of Pearson correlation analyses. We used STATISTICA 7.0 for all statistical analyses. Throughout the paper means are reported ± 1 SD.

Results

Mean acorn production was 36.81 ± 34.14 , 51.64 ± 52.18 , 47.63 ± 69.43 acorns m^{-2} in 1997, 1998 and 1999, respectively. Production ranged from 0 to 300 acorns m^{-2} . Fig. 1 shows acorn production for each individual tree as an average over the three study years in each stand. Stand A showed the highest average acorn production and stand D the lowest. Coefficients of variation (CV) were 1.26, 0.93, 1.00 and 0.95 for stands A, B, C and D, respectively. Despite this, acorn production was homogeneous among different sites and years (Table 1).

The proportion of sound acorns for the whole study period was 67.00%, which differed among years (Table 1). The mean percentage of acorns infested by insect and pathogens was 19.69% for all individuals and study years pooled. On average, *Curculio* infested 7.64% of acorns, *Cydia* 1.76% and *Brenneria* 10.29%. These rates did not vary significantly among different stands. However, we found a significant annual varia-

tion for the *Cydia* damage, which was consistent across stands in view of the non-significant Year \times Stand interaction (Table 1). The rate of predation by *Cydia* only differed among the years 1997 and 1998, with values of 0.79% and 3.08%, respectively (Fig. 2). Other significant annual variation was found for the damage by *Curculio*, which varied across the stands since a significant effect was observed when we analyzed year and stand jointly (Table 1). Predation of acorns by *Curculio* ranged from 4.5% in the year 1999 to 13.8% in 1998 (Fig. 2). The rate of *Brenneria* damage did not change either among stands or years.

Regarding the relationship between these different pre-dispersal agents, *Curculio* was related linearly and positively to *Cydia* in 1997 and 1999 (Table 2). The remaining pests were independent from each other in every year (Pearson's correlation, $p > 0.05$; all stands pooled; Table 2).

The percentage of acorns infested by the different agents did not fit any of the hypothesized linear (Pearson's correlation, $0.110 < p > 0.927$) or non-linear functions (exponential function, $0.018 < R^2 > 0.315$; $0.927 < p > 0.110$). Therefore, damage was independent of tree acorn production (Fig. 3). Only the rate of acorns infested by *Cydia* in 1999 showed a significant exponential relationship ($R^2 = 0.476$, $p = 0.009$) (Fig. 3).

Discussion

Crop size of acorns in dehesas

Mean values of holm oak acorn production obtained in this study by means of seed traps (44.60 acorns m^{-2})

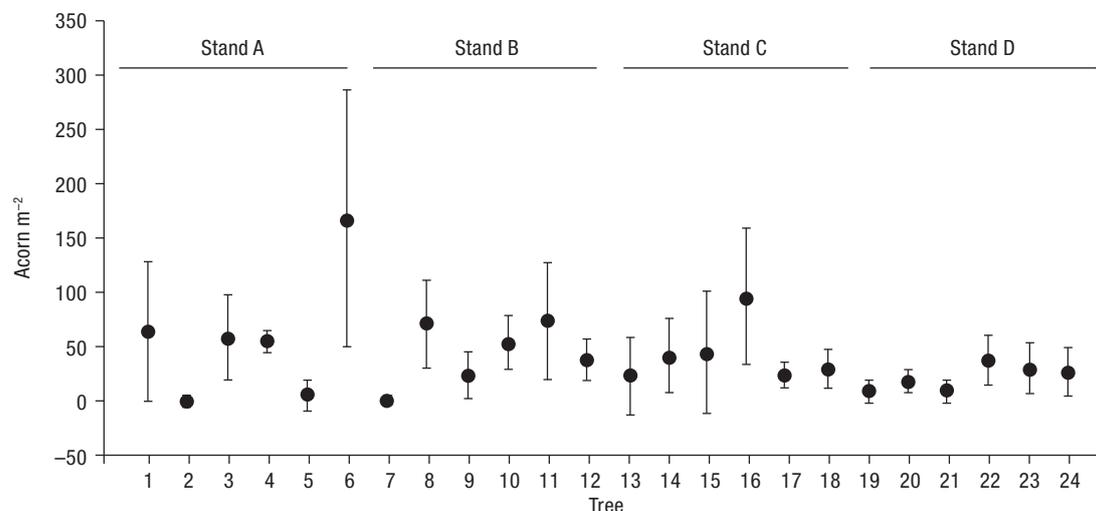


Figure 1. Mean acorn production (acorn m^{-2}) by each tree and stand. Vertical bars show standard deviation.

Table 1. Results from GLM analyses on a repeated-measured ANOVA-type design testing for the effects of year, stand and year \times stand on acorn production, sound acorn and acorn damages

	Year		Stand		Year \times Stand	
	F _{2,68}	p	F _{3,67}	p	F _{6,64}	p
Production	0.725	0.491	1.044	0.397	3.640	0.006
% Sound acorns	7.931	0.001	0.064	0.978	1.435	0.227
% Infested <i>Cydia</i>	4.930	0.012	1.064	0.388	0.865	0.529
% Infested <i>Curculio</i>	11.493	0.000	0.986	0.420	2.326	0.052
% Infested <i>Brenneria</i>	2.162	0.129	1.639	0.214	0.712	0.642

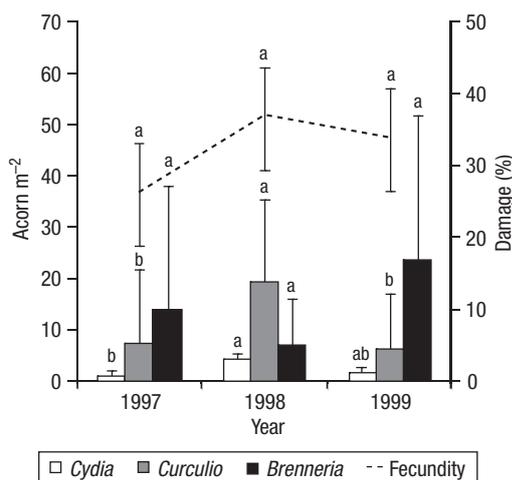
were lower than those found in dehesas using the same method by Rivest *et al.* (2011) and it was very similar to those found by Díaz *et al.* (2009) and Alejano *et al.* (2011) (Table 3). Since most studies in dehesas have reported acorn production values as acorn mass per area unit, to compare our results with those obtained elsewhere we transformed our data by multiplying acorn number per the mean fresh acorn mass in the study area ($6.5 \text{ g} \pm 1.39 \text{ SD}$; Pulido, 1999). As shown in Table 3, acorn production, expressed as mass per

unit area (289.9 g m^{-2}) was within the range of values reported by other authors in dehesas ($119.7\text{-}357.5 \text{ g m}^{-2}$), and above values given for forest and dehesas with pollarded trees (Table 3). All these studies (included ours) report a huge variability between trees.

Variation in acorn production

Our data showed no significant differences between stands within the dehesa farm studied, contradicting the hypothesis 1. At first glance this could be due to the huge variability in acorn production shown by individual trees within stands. Thus, individual acorn production ranged from 0 to 300 in stand A, 0 to 142 in stand B, 0 to 162 in stand C, and 0 to 60 acorns m^{-2} in stand D. Under these conditions, significant differences were unlikely to be found even with greater sample sizes within stands. This extreme individual variability has been already reported in previous studies (*e.g.*, Torres *et al.*, 2004; García-Mozo *et al.*, 2007). Therefore, it can be concluded that differences among paddocks, either due to edaphoclimatic conditions or management, did not translate into noticeable differences in acorn crops.

At a spatial scale similar to that used in our study, Martín-Vicente *et al.* (1998) found differences of acorn production between mixed stands of *Q. ilex*, *Q. suber* and *Q. canariensis*, but in this case acorn production

**Figure 2.** Annual variations of acorn production (acorn m^{-2}) and insect and pathogen damage in the three study years. Vertical bars show standard deviation. Different letters indicate significant differences between years (LSD test at $p \leq 0.05$).**Table 2.** Pearson correlation coefficients for the relationships between different kind of insect and pathogen damage in the three study years

	1997		1998		1999	
	r	p	r	p	r	p
<i>Cydia</i> (%) - <i>Curculio</i> (%)	0.476	0.022	0.299	0.165	0.435	0.034
<i>Cydia</i> (%) - <i>Brenneria</i> (%)	0.339	0.114	-0.032	0.885	0.296	0.160
<i>Curculio</i> (%) - <i>Brenneria</i> (%)	0.284	0.188	0.157	0.474	0.315	0.134

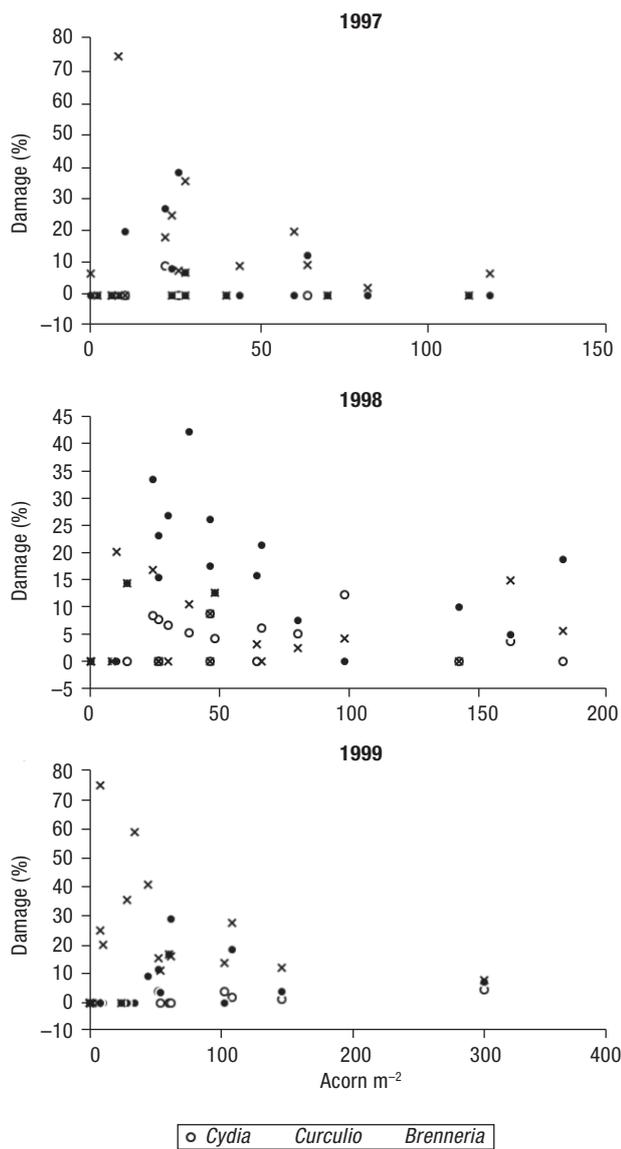


Figure 3. Relationships between acorn production (acorn m⁻²) and proportion of acorns damaged by *Cydia*, *Curculio* and *Brenneria* in years 1997, 1998 and 1999. All stands pooled.

could be compensated between different species. In North American oak species Peter and Harrington (2009) observed differences at the level of local populations in *Q. garryana*, whereas Liebhold *et al.* (2004) reported synchrony between trees over distances less than 10 km in different *Quercus* species. In other oak species a trend of acorn production to synchronize over large geographic areas has been established (Sork *et al.*, 1993; Healy *et al.*, 1999; Koenig and Knops, 2000). Due to the limited number of years in our annual series we did not evaluate any synchrony coefficient. Nevertheless, the lack of spatial variability detected, and its

consistency over time, would imply spatial synchrony at least at the farm level. This result implies that spatial differences would be detected at a larger (regional or geographical) scale. This is in agreement with most long-term studies on spatial synchrony. Thus, Peter and Harrington (2009) reported synchrony up to a radius of 33 km. In holm-oak, studies from local to geographical scales are clearly needed to clarify the extent of spatial synchrony and its implication for tree and livestock management.

Variation in acorn damage

Though many studies have estimated the pre-dispersal losses of acorns caused by *Curculio* weevils, *Cydia* moths and *Brenneria* disease (Soria *et al.*, 1999; Vázquez *et al.*, 1999; Pulido and Díaz, 2005), few studies have addressed to what extent these losses fit any spatial pattern. Concerning acorn losses, it must be noted that studies based on acorns collected on the ground tend to overestimate acorn damage, as sound acorns are selected by post-dispersal predators (Bonal and Muñoz, 2007). In our study, based on acorns collected from the canopy, the mean attack rate by both insects was 9.40%, that is well below figures reported in comparable studies in holm-oak in dehesas: 18% (Pulido and Díaz, 2005), 58% (Bonal *et al.*, 2007), and 20% in Pulido *et al.* (2010). On the other hand, *Brenneria* infested 10.29% of acorns, a figure lower than the 16.30% found by Pulido and Díaz (2005) and 25.60% reported by Vázquez *et al.* (1999). As previous studies have found (Bonal *et al.*, 2007; Díaz *et al.*, 2009), our analysis show extreme individual variation in the impact of all these damages, which could be related to individual variation in the defensive mechanisms elicited by holm oaks facing damage (Díaz and Pulido, 1995; Díaz *et al.*, 2004).

The levels of infestation did not vary between different stands, a result contradicting previous studies and the hypothesis 3. Thus, Jiménez *et al.* (2008), analyzing the spatial distribution of *Curculio* populations in a dehesa of southern Spain, concluded that the spatial distribution was heterogeneous in space but stable over time. Leiva and Fernández-Alés (2005) in a nearby area found differences among stands in dehesas and shrublands. In forests from northern China significant spatial and temporal heterogeneity of acorn damage by insects in *Q. liaotungensis* was established in relation to topography (Yu *et al.*, 2003). Therefore, spatial hete-

Table 3. Acorn production of holm-oak collected in traps according to different authors. Data are averages of several years and sites. DM and FM are dry mass and fresh mass, respectively

Reference	Habitat	Acorn production			
		No./m ²	g/m ² (DM)	g/m ² (FM)	No./tree ¹
Current study	Dehesa	44.60		289.90	
Gómez <i>et al.</i> (1980)	Dehesa		86.60	145.03*	
Martín-Vicente <i>et al.</i> (1998)	Dehesa		200.80	338.62*	
Torres <i>et al.</i> (2004)	Dehesa		177.20	298.82*	
Pulido (1999)	Dehesa				5,715.15
	Forest				646.95
Bonal <i>et al.</i> (2007)	Dehesa				8,831
Cañellas <i>et al.</i> (2007)	Dehesa		145.28	245*	
	Dehesa ¹		73.18	123.41*	
Díaz <i>et al.</i> (2009)	Forest	10		65	538
	Dehesa	55		357.5	
Carevic <i>et al.</i> (2010)	Dehesa			339.70	
Pérez-Ramos <i>et al.</i> (2010)	Forest		0.3-180.6	0.51-304.55*	
Alejano <i>et al.</i> (2011)	Dehesa ¹	43.98		238.83	
Rivest <i>et al.</i> (2011)	Dehesa	50-73	71-119	119.73-200.67*	

¹ Pollarded trees. * Dry mass transformed in fresh mass according to dry matter percentage reported by Nieto *et al.* (2002).

rogeneity seems to be the rule in acorn-insect interactions, a point that deserves further research in dehesa systems. In our case, as there is a positive effect in the stand and year interaction in *Curculio* damage, it could be possible that in some stand the *Curculio* damage varies along the time.

Our results showed that acorn infestation by each insect species varied among years. Many authors have explained temporal variation in relation with predator satiation in peak years of acorn production, while predators would starve in low year of the masting interval (Kelly, 1994; Crawley and Long, 1995; Kelly and Sork, 2002; Espelta *et al.*, 2009). We found significant temporal variation in the attack rate of insects acorn predators despite non-significant variation in acorn production. It can be hypothesized that climatic conditions might underlie the differences in infestation found between years, pest population fluctuating due to temperature (Manel and Debouzie, 1997) and precipitation (Debouzie *et al.*, 2002; Soula and Menu, 2003). These environmental factors could also explain the lack of relationship between the rate of infestation and the annual acorn crop size per tree found in this study (see also Pulido and Díaz, 2005, for *Q. ilex* and Fukumoto and Kajimura, 2011, for *Q. variabilis*).

Concerning the relationship between different agents infesting acorns, only *Cydia* and *Curculio* were related to each other in the years with lower acorn pro-

duction. Both species are very selective when ovipositing (Soria *et al.*, 1999), in such a way that trees with better acorns could be attacked more severely by both insects. However, other authors did not found any relationship between them (Pulido, 1999; Soria *et al.*, 1999); the effect of interference between these species can be weaker in years with high acorn production (Pulido, 1999). On the other hand, *Curculio* appears to be a vector of *Brenneria* (Pérez-Laorga *et al.*, 2005) but we did not detect any relation. The general lack of interactions between acorn pests could be explained also by the low levels of infestation found in this study.

To end up, the results obtained in this study highlight several points related to holm oak management in dehesas. First, huge individual variation between trees does not necessarily translate into significant differences between stands or paddocks within a farm. Second, estimation of the rates of acorn damage should rely on acorns still attached to the canopy, as acorns collection in the ground tend to overestimate attack rates. Finally, since damages between *Curculio* and *Cydia* seem to be related, joint measures could be designed to reduce their impact.

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