

# Acorns of invasive Northern Red Oak (*Quercus rubra*) in Europe are larval hosts for moths and beetles

Łukasz Myczko · Łukasz Dylewski · Artur Chrzanowski · Tim H. Sparks

Received: 8 December 2016 / Accepted: 7 May 2017 / Published online: 19 May 2017  
© The Author(s) 2017. This article is an open access publication

**Abstract** In their first phase of expanding into new areas, invasive plants often take advantage of the inability of existing herbivores and pathogenic species to exploit them. However, in the longer term local enemies may adapt to using these invasive species as a food source. This study assesses the use of mature acorns of two oak species in Europe (the native Pedunculate Oak *Quercus robur* and the invasive Northern Red Oak *Quercus rubra*) by moths *Cydia fagiglandana* and *Cydia splendana* and beetles *Curculio* spp. We show that acorns of invasive oak species can be equally attractive to *C. splendana* but only partially so to *C. fagiglandana* where infestation rates were significantly lower (approximately half) compared to the native oak. The infestation by *Curculio* beetles of Northern Red Oak was marginal, less than 1% of the rate in the native oak species. The larval final weights did not differ significantly between host

species, but emergence of *C. splendana* and *Curculio* spp. took significantly longer in acorns of Northern Red Oak. It is likely that *C. fagiglandana* and *C. splendana* have increased their niche breadths by exploiting invasive oak species and avoiding competition with the *Curculio* weevils. Furthermore, the occurrence of Northern Red Oak could stabilize food resources during years when native oak species have poor acorn crops.

**Keywords** Invasive plant species · Seed damage · Seed loss · Acorns

## Introduction

A substantial proportion of deciduous tree species growing in the temperate zone of the Northern Hemisphere produce seeds with large energy reserves that allow their seedlings to successfully compete with other plants. However, such heavy seeds are also a plentiful food resource used by many animals, both invertebrate and vertebrate, which results in high pre- and post-dispersal seed losses (e.g., Jimenez-Pino et al. 2011; Bonal et al. 2012; Bieberich 2016). High seed predation together with abiotic factors in some habitats are able to prevent successful regeneration of forest trees (Pulido and Díaz 2005). Oaks (*Quercus* spp.) are widely distributed Palearctic species which have large seeds in the form of acorns. The main pre-

---

Ł. Myczko (✉) · Ł. Dylewski · T. H. Sparks  
Institute of Zoology, Poznań University of Life Sciences,  
Wojska Polskiego 71 C, 60-625 Poznań, Poland  
e-mail: lukasz.myczko@up.poznan.pl

A. Chrzanowski  
Department of Forest Entomology, Poznań University of  
Life Sciences, Wojska Polskiego 71 C, 60-625 Poznań,  
Poland

T. H. Sparks  
Faculty of Engineering, Environment and Computing,  
Coventry University, Priory Street, Coventry CV1 5FB,  
UK

dispersal predators which strongly limit the reproductive success of oaks are insects, mainly *Curculio* beetles (Coleoptera: Curculionidae) and *Cydia* moths (Lepidoptera: Tortricidae) which infest a large proportion of the produced seeds (e.g., Gibson 1981; Jimenez-Pino et al. 2011; Bonal et al. 2012). Even if the seeds do not completely lose their ability to germinate, the fitness of seedlings from such infected seeds is significantly reduced by insect feeding compared to sound seeds (Bonal et al. 2007; Perea et al. 2012). Such significant losses during reproduction have caused a number of morphological and chemical characteristics to evolve that serve as defense mechanisms against seed predators. One of these basic tree strategies is the occurrence of mast years, alternating with periods of very low seed production (Selås 1997), which are spatially synchronized over large areas (Koenig et al. 2013). This strategy reduces the availability of food in the years of limited seed production, which results in a decrease in the number of seed predating animals.

However, such a strategy is not fully effective against polyphagous species that in the absence of one species are able to develop in the seeds of other species. Examples of such species are the moths *Cydia splendana* and *Cydia fagiglandana* which can develop in the seeds of relatively numerous trees such as oaks (*Quercus* spp.), Sweet Chestnut (*Castanea sativa*) and European Beech (*Fagus sylvatica*) (Bovey 1966; Bradley et al. 1979). North of the geographical distribution of Sweet Chestnut, the larvae of *C. fagiglandana* feed on beech nuts and the larvae of *C. splendana* on acorns. Both moth species are found on Sweet Chestnut in southern Europe, where they cause significant damage (Bovey 1966; Bradley et al. 1979).

In their initial colonising phase, invasive species often take advantage of the inability of existing herbivores and pathogenic species to control them. During this period, invasive species should impact negatively on herbivores, because the invasive species compete for resources and space with native plants which are the natural food resources for the herbivores (Agrawal et al. 2005; Liu and Stiling 2006; Huang et al. 2010; Dai et al. 2014). Some interactions with local animals may be positive for invasive plant species and facilitate faster colonization, for example the long distance dispersion of Northern Red Oak (*Quercus rubra*) by the European Jay (*Garullus glandarius*) (Myczko et al. 2014). But, the longer

they have been in an area the greater the chance that local enemies will have adapted to use the invasive species as a food source (Shea and Chesson 2002). Additionally the probability of successful colonization an exotic tree in the second range by the native insects increase with presence of congeneric native trees in environment (Roques et al. 2006; Branco et al. 2015). A large proportion of new enemies are recruited from polyphagous species (Roques et al. 2006; Branco et al. 2015). Therefore, the appearance of additional non-native tree species in the environment does not always result in a reduction in niche quality arising from a decrease in natural food resources replaced by invasive species. However, if herbivores adapt to feeding on invasive plant species the quality of the niche can increase because of an increased niche breadth. Adapting to a new food source can reduce competition for nutrients between species that compete for traditional food resources provided by the old host. Such a situation exists in Central Europe where the invasive species Northern Red Oak competes with native oaks (Major et al. 2013; Woziwoda et al. 2014). The occurrence and natural regeneration of Northern Red Oak in forests significantly reduces native species richness and abundance. No vascular plant species is known to benefit from co-occurring with Northern Red Oak, moreover the abundance of this invasive oak strongly limits natural restocking of all native woody species (Woziwoda et al. 2014).

The main aim of our study was to compare the use of acorns of two species of oak, one native and one invasive, to determine if there has been an adaptation to use the new oak species as a foraging source. We hypothesize that they may share the same acorn herbivores. Additionally we suggest that this information has important ecological implications for the population dynamics of the native herbivorous species by increasing their niche breadth. Moreover, indirect effects on native plant species are also possible by increasing the infestation of seeds because of a higher more stable feeding niche of herbivores.

## Methods

We selected five areas in central Wielkopolska, Poland (52°26'–52°36'N; 16°48'–17°03'E) which were separated from one another by 3.6–21.4 km. In each area, mature trees of Pedunculate Oak and Northern Red

Oak both grew together, and in each area we randomly chose 10 fruiting trees of each species and collected 100 acorns from each tree. We collected fallen acorns on 21 September 2014 during the period of maximum seed rain. We decided on this strategy because despite the different development strategy of acorns (taking one or two years) seed rain takes place at the same time. Acorns from each species and each area were bulked into a container of 1000 acorns. Acorns were kept in the laboratory at 10 °C and each day we removed larvae that had emerged from them. Larvae were collected from each container until two consecutive days produced no larvae; this took 41 days. For each larvae we recorded the species of oak, the number of days since the beginning of the experiment, their fresh weight and determined the genus or species. Larvae were weighed to a accuracy of 0.1 mg using an analytical balance (Sartorius® BP 160P), no later than 24 h after leaving the acorn. Because of the absence of morphological features to determine to species level, *Curculio* larvae were recorded to genus level only. The species of genera *Curculio* occurring in Poland and related to oak species are: *Curculio glandium*, *Curculio venosus*, *Curculio pellitus* and *Curculio elephas* (Burakowski et al. 1995). However, in the case of *Cydia* caterpillars we determined the species using the colour of the body and the number of crochets on prolegs according to Brown and Komai (2008).

### Statistical analysis

For each insect species/group, Chi square contingency tests were used to compare numbers of larvae between the two *Quercus* species. To test differences in the time to emerge for larvae between Pedunculate Oak and Northern Red Oak acorns we used t tests of each species (*Cydia*) or genus (*Curculio*). We used GLMs with a Gaussian error distribution to analyse larval weight in relation to two predictor variables: oak species and days until emergence, and their interaction. Analysis and graphs were produced using R 3.2.3 (R Core Team 2015) using the ggplot2 package (Wickham 2009).

### Results

*Cydia fagiglandana* showed a significant preference to develop in acorns of Pedunculate Oak, however a substantial number of individuals also developed in

Northern Red Oak acorns. In contrast, the number of *C. splendana* larvae did not differ significantly between the two oak species. However, almost all *Curculio* species developed in Pedunculate Oak acorns; less than 0.4% of the total identified *Curculio* larvae developed in Northern Red Oak acorns (Table 1).

There were no significant differences between the two oak species in the speed of larval emergence of *C. fagiglandana*. In contrast, *C. splendana* and *Curculio* species larvae emerged from Northern Red Oak acorns significantly later than from Pedunculate Oak acorns (Table 2). The larval weights (mean  $\pm$  SE [mg]) developed in Pedunculate Oak acorns were as follows: *C. fagiglandana* (48.0  $\pm$  0.6), *C. splendana* (36.1  $\pm$  1.1) and *Curculio* species (35.2  $\pm$  0.4). In Northern Red Oak the mean larval weights were: *C. fagiglandana* (46.0  $\pm$  0.9), *C. splendana* (33.7  $\pm$  0.9) and *Curculio* species (31.5  $\pm$  4.3).

With the exception of *C. fagiglandana*, larval body weight wasn't dependent on the number of days until emergence and in no insect species was there a significant difference in mean larval weight between the oak species (all  $p > 0.05$ , Table 3). For *C. fagiglandana* the average larval body weight significantly decreased with increasing days to emergence (Table 3).

### Discussion

Acorns of both Pedunculate Oak and Northern Red Oak are hosts for the development of *C. fagiglandana*, *C. splendana* and also *Curculio* weevil larvae. However, there are significant differences in the prevalence of these invertebrates in the acorns of the two studied oak species. Larval stages of the moth species *C. fagiglandana* and *C. splendana* occur in considerable numbers in Northern Red Oak acorns, and for *C. splendana* there was no significant difference in numbers between the two oak species. The use of Northern Red Oak acorns may help to avoid competition with *Curculio* weevil larvae, which has been described previously in the case of *C. fagiglandana* (Jimenez-Pino et al. 2011). In that study, inter-specific competition with the weevil *C. elephas* was the factor that most affected the spatial distribution of *C. fagiglandana* larvae (Jimenez-Pino et al. 2011). Apart from reduced competition with other seed eating

**Table 1** The number of larvae developing in Pedunculate Oak and Northern Red Oak acorns from 5000 acorns of each species

|                        | Pedunculate Oak<br>N | Northern Red Oak<br>N | $\chi^2$ | <i>p</i> |
|------------------------|----------------------|-----------------------|----------|----------|
| <i>C. fagiglandana</i> | 235                  | 119                   | 38.01    | <0.001   |
| <i>C. splendana</i>    | 130                  | 140                   | 0.37     | 0.543    |
| <i>Curculio</i> spp.   | 2788                 | 11                    | 2755.17  | <0.001   |

Differences in the proportions inhabiting the acorns of the two oaks were tested using  $\chi^2$  tests

**Table 2** The mean number of days spent post-collection by larvae in Pedunculate Oak and Northern Red Oak acorns from 5000 acorns of each species

|                        | Pedunculate Oak<br>Mean $\pm$ SE | Northern Red Oak<br>Mean $\pm$ SE | t    | df   | <i>p</i> |
|------------------------|----------------------------------|-----------------------------------|------|------|----------|
| <i>C. fagiglandana</i> | 4.7 ( $\pm$ 5.4)                 | 5.2 ( $\pm$ 5.3)                  | 0.84 | 352  | 0.401    |
| <i>C. splendana</i>    | 7.4 ( $\pm$ 9.2)                 | 14.4 ( $\pm$ 9.4)                 | 6.21 | 268  | <0.001   |
| <i>Curculio</i> spp.   | 9.7 ( $\pm$ 8.3)                 | 21.0 ( $\pm$ 11.7)                | 4.46 | 2797 | <0.001   |

Differences in the time to emergence in the acorns of the two oaks were tested using t tests

**Table 3** Factors affecting the body weight of the larvae of moths and beetles

| Variable                  | Larvae species         |          |          |                     |          |          |                      |          |          |
|---------------------------|------------------------|----------|----------|---------------------|----------|----------|----------------------|----------|----------|
|                           | <i>C. fagiglandana</i> |          |          | <i>C. splendana</i> |          |          | <i>Curculio</i> spp. |          |          |
|                           | <i>df</i>              | <i>F</i> | <i>p</i> | <i>df</i>           | <i>F</i> | <i>p</i> | <i>df</i>            | <i>F</i> | <i>p</i> |
| Intercept                 | 1                      | 4280.78  | <0.001   | 1                   | 1088.10  | <0.001   | 1                    | 21.28    | <0.001   |
| Oak species (O)           | 1                      | 0.77     | 0.380    | 1                   | 2.98     | 0.085    | 1                    | 0.12     | 0.732    |
| Days until emergence (DE) | 1                      | 17.45    | <0.001   | 1                   | 2.17     | 0.142    | 1                    | 0.41     | 0.522    |
| O * DE                    | 1                      | 0.26     | 0.609    | 1                   | 1.62     | 0.205    | 1                    | 0.02     | 0.894    |

insects the ability to develop larvae in the tissues of another host plant can increase the stability of the population. Our forest trees are characterized by the presence of mast years and years with poor production of seeds (Kantorowicz 2000). As a result, there are alternate years suitable for the development and increase of the invertebrate population and years when the availability of seeds is very limited causing a decrease in population size (Selås 1997). Of course, animals have evolved mechanisms to survive such adverse periods; an example is prolonged diapause in *Curculio* weevils which stabilizes the local population by surviving the unfavorable period in the pupal stage and developing into the adult insect in subsequent years (Menu, Roebuck and Viala 2000; Menu and

Desouhant 2002). However, a lack of data on the occurrence of this mechanism in the case of *Cydia* spp. suggests a different strategy based on adapting to a greater number of host plants. More larval host species results in a greater stability of food resources and makes a drastic reduction of the population, due to the lack of fruiting of suitable food plants in some years, much less likely. Thus, the introduction by humans of additional invasive species into the environment has increased the stability of the local population of *C. splendana* and *C. fagiglandana*. An advantage for insects able to develop in acorns of the invasive species Northern Red Oak is that the acorns mature after 2 years, unlike native Oaks in this part of Europe where maturation takes place in the same growing

season as flowering. This difference has a significant impact on the occurrence of seed years (Koenig and Knops 2000) and the presence of oaks of asynchronous acorn production helps to stabilize populations of generalists (Fukumoto and Kajimura 2011). Thus, the introduction of invasive species into the environment may have a positive impact on acorn-developing insects. Additionally, this process can be reinforced by anthropogenic fragmentation of habitats, significantly increasing seed production and seed size (Bonal et al. 2012). Moreover, climate change may also disrupt the occurrence of mast years (Selås 1997).

The results of our study show that *Curculio* weevils in Northern Red Oak acorns in Poland are extremely rare. Therefore, seed losses associated with feeding by insects in acorns are several times lower in comparison with the native oak, in which infestation of acorns by *Curculio* weevils is many times greater than that of other species of insects. The development of larvae in the acorn does not always mean a failure to germinate. However, infestation by an insect causes a significant decrease in the ability to germinate, for example germination of sound Northern Red Oak acorns was 86% but only 26% in the case of weevil-damaged acorns. In addition, seedlings developing from infected acorns had a significantly lower fitness (Lombardo and McCarthy 2009). In the case of natural regeneration, the development of *Curculio* larvae in the acorn not only directly affects the plant's survival, but also indirectly reduces its fitness by reducing the likelihood of seed dispersal by animals. Infested acorns are more often dispersed than those from which larvae have emerged, however both are still significantly less dispersed than sound acorns (Perea et al. 2012). However, it should be remembered that dispersal by animals is also affected by other factors, such as the species of acorn (Myczko et al. 2014; Bonacchi et al. 2015).

Marginal infestation of acorns by *Curculio* weevils supports the enemy release hypothesis during the colonization of new areas by invasive species which is often assisted by the lack of natural herbivores and pathogens, as well as the inability of naturally existing herbivores and pathogenic species to control the invasive organisms (Agrawal et al. 2005; Liu and Stiling 2006; Huang et al. 2010; Dai et al. 2014). An additional argument in the case of Northern Red Oak enemy release hypothesis is that, in its natural range,

Northern Red Oak averages over 52% acorns damaged by insects, mainly by *Curculio* weevils (Gibson 1981). However, these were different weevil species than occur in Europe. Currently available data do not support the conclusion that in the long term European species of *Curculio* weevils will adapt to develop in the acorns of Northern Red Oak. However, the very few *Curculio* weevil larvae in our sample of Northern Red Oak acorns suggests the possibility of such a scenario.

One of the most important features that is easy to measure in the case of insect larvae is their weight, this measurement is very strongly correlated with fitness. The higher weight of pre-imaginal stages strongly influences the fecundity of females (Calvo and Molina 2005) and also positively influences reproductive success of males (e.g., Klingenberg and Spence 1997). The weight of larvae emerging from acorns reflects their fitness and also the quality of their food. Our results indicate no significant effect of the species of oak on the larval weight emerging from acorns, which means *Cydia* species can develop in the non-native host species to reach the same level of fitness as in the native oak. However, achieving this mean weight takes significantly longer in the case of *C. splendana* and *Curculio* weevils (Table 2) in the non-native oak species, which means a lower performance. *C. splendana* and *Curculio* spp. take longer to develop on Northern Red Oak acorns in comparison with Pedunculate Oak acorns, and they will also then be exposed to increased probability of consumption by animals foraging on acorns, such as wild boars and small mammals (Focardi et al. 2000). The results shown in Table 3 indicate that, with the exception of *C. fagiglandana*, the final mean weight of insects was not influenced by duration within the acorn. However, in *C. fagiglandana* the average weight of larvae significantly decreased with the number of days elapsed. This suggests that *C. fagiglandana* prefers to leave acorns earlier, reducing the risk of being predated by animals feeding on acorns even if the larvae had not reached optimum weight.

In conclusion, we clearly show that a new element of the European flora is currently used as a foraging substrate by local moths and beetles, and can probably stabilize local trophic niches of *C. splendana* and *C. fagiglandana*.

**Acknowledgements** We wish to thank Piotr Tryjanowski for very helpful comments on the manuscript. We would like to thank the reviewers for their comments, which have resulted in a much-improved manuscript. We thank Forest Services from the Puszcza Zielonka and Poznań Forests for access to the forest stands.

**Open Access** This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

## References

- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos J (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86:2979–2989. doi:10.1890/05-0219
- Bieberich J (2016) Acorns of introduced *Quercus rubra* are neglected by European Jay but spread by mice. *Ann For Res* 59:1–10. doi:10.15287/afr.2016.522
- Bonacchi A, Bartolommei P, Gasperini S, Manzo E, Cozzolino R (2015) Acorn choice by small mammals in a Mediterranean deciduous oak forest. *Ethol Ecol Evol*. doi:10.1080/03949370.2015.1089326
- Bonal R, Munoz A, Díaz M (2007) Satiation of predispersal seed predators: the importance of considering both plant and seed levels. *Evol Ecol* 21:367–380. doi:10.1007/s10682-006-9107-y
- Bonal R, Hernandez M, Ortego J, Munoz A, Espelta JM (2012) Positive cascade effects of forest fragmentation on acorn weevils mediated by seed size enlargement. *Insect Conserv Diver* 5:381–388. doi:10.1111/j.1752-4598.2011.00172.x
- Bovey P (1966) Super-famille des Tortricidae. In: Balachowsky AS (ed) *Entomologie Appliquée à l'Agriculture*, vol II. Masson, Paris, pp 456–893
- Bradley JD, Tremewan WG, Smith A (1979) British tortricoid moths. Tortricidae: Olethreutinae. The Ray Society, London
- Branco M, Brockerhoff EG, Castagneyrol B, Orazio C, Jactel H (2015) Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. *J Appl Ecol* 52:69–77. doi:10.1111/1365-2664.12362
- Brown JW, Komai F (2008) Key to larvae of castanea-feeding olethreutinae frequently intercepted at US ports-of-entry (Lepidoptera: Tortricidae). *Tropical Lepidoptera* 18:2–4
- Burakowski B, Mroczkowski M, Stefańska J (1995) *Chrzyszczce - Coleoptera. Ryjkowce - Curculionidae, część 2. Katalog Fauny Polski tom: XXIII, Warszawa*
- Calvo D, Molina JM (2005) Fecundity–body size relationship and other reproductive aspects of *Streblothele panda* (Lepidoptera: Lasiocampidae). *Ann Entomol Soc Am* 98: 191–196. doi:10.1603/0013-8746(2005)098[0191:FSRA OR]2.0.CO;2
- Dai H, Lu X, Zhang J, Ding J (2014) Responses of a native beetle to novel exotic plant species with varying invasion history. *Ecol Entomol* 39:118–124. doi:10.1111/een.12072
- Focardi S, Capizzi D, Monetti D (2000) Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. *J Zool* 250:329–334. doi:10.1111/j.1469-7998.2000.tb00777.x
- Fukumoto H, Kajimura H (2011) Effects of asynchronous acorn production by co-occurring *Quercus* trees on resource utilization by acorn-feeding insects. *J For Res* 16:62–67. doi:10.1007/s10310-010-0208-7
- Gibson LP (1981) Insects that damage northern red oak acorns. US Forest service research paper NE-492, p 6
- Huang W, Siemann E, Wheeler GS, Zou J, Carrillo J, Ding J (2010) Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *J Ecol* 98:1157–1167. doi:10.1111/j.1365-2745.2010.01704.x
- Jimenez-Pino A, Maistrello L, Lopez-Martinez MA, Ocete-Rubio ME, Soria-Iglesias FJ (2011) Spatial distribution of *Cydia fagiglandana* (Zeller) in an exploited holm oak (*Quercus ilex* L.) forest. *Span J Agric Res* 9:570–579. doi:10.5424/sjar/20110902-050-10
- Kantorowicz W (2000) Half a century of seed years in major tree species of Poland. *Silvae Genet* 49:245–248
- Klingenberg CP, Spence J (1997) On the role of body size for life-history evolution. *Ecol Entomol* 22:55–68. doi:10.1046/j.1365-2311.1997.00031.x
- Koenig WD, Knops JM (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. *Am Nat* 155:59–69. doi:10.1086/303302
- Koenig WD, Díaz M, Pulido F, Alejano R, Beamonte E, Knops JM (2013) Acorn production patterns. In: Campos P, Huntsinger L, Oviedo JL, Starrs PF, Díaz M, Standiford RB, Montero G (eds) *Mediterranean oak woodland working landscapes: dehesas of Spain and ranchlands of California*. Springer, New York, pp 181–209
- Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biol Invasions* 8:1535–1545. doi:10.1007/s10530-005-5845-y
- Lombardo JA, McCarthy BC (2009) Seed germination and seedling vigor of weevil-damaged acorns of red oak. *Can J For Res* 39:1600–1605. doi:10.1139/X09-079
- Major KC, Nosko P, Kuehne C, Campbell D, Bauhus J (2013) Regeneration dynamics of non-native northern red oak (*Quercus rubra* L.) populations as influenced by environmental factors: a case study in managed hardwood forests of southwestern Germany. *For Ecol Manag* 291:144–153. doi:10.1016/j.foreco.2012.12.006
- Menu F, Desouhant E (2002) Bet-hedging for variability in life cycle duration: bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* 132:167–174. doi:10.1007/s00442-002-0969-6
- Menu F, Roebuck JP, Viala M (2000) Bet-hedging diapause strategies in stochastic environments. *Am Nat* 155:724–734. doi:10.1086/303355
- Myczko Ł, Dylewski Ł, Zduńiak P, Sparks TH, Tryjanowski P (2014) Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species

- (Northern Red Oak *Quercus rubra*) in Europe. For Ecol Manag 331:35–39. doi:[10.1016/j.foreco.2014.07.027](https://doi.org/10.1016/j.foreco.2014.07.027)
- Perea R, López D, San Miguel A, Gil L (2012) Incorporating insect infestation into rodent seed dispersal: better if the larva is still inside. Oecologia 170:723–733. doi:[10.1007/s00442-012-2350-8](https://doi.org/10.1007/s00442-012-2350-8)
- Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. Ecoscience 12:92–102. doi:[10.2980/i1195-6860-12-1-92.1](https://doi.org/10.2980/i1195-6860-12-1-92.1)
- R Development Core Team (2015) R: a language and environment for statistical computing. Vienna, Austria
- Roques A, Auger-Rozenberg MA, Boivin S (2006) A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. Can J For Res 36:299–313. doi:[10.1139/x05-277](https://doi.org/10.1139/x05-277)
- Selås V (1997) Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. Oikos 80:257–268. doi:[10.2307/3546594](https://doi.org/10.2307/3546594)
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176. doi:[10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Wickham H (2009) ggplot2: Elegant graphics for data analysis. Springer, New York
- Woziwodza B, Kopeć D, Witkowski J (2014) The negative impact of intentionally introduced *Quercus rubra* L. on a forest community. Acta Soc Bot Pol 83:39–49. doi:[10.5586/asbp.2013.035](https://doi.org/10.5586/asbp.2013.035)