

Plant-animal interactions in dynamic environments: how tree
masting and nitrogen deposition affect consumer populations,
seed dispersal and seed predation

Michał Bogdziewicz

PhD Thesis

Faculty of Biology

Adam Mickiewicz University in Poznań

2016, Poznań

The thesis has been prepared at the Department of Systematic Zoology

© ZZS 2016, Poznań

Supervisor:

Dr. hab. Rafał Zwolak

Department of Systematic Zoology, Institute of Environmental Biology, Faculty
of Biology, Adam Mickiewicz University, Poznań, Poland

CONTENTS

- I. Streszczenie
- II. Summary
- III. Doctoral dissertation
- IV. Authorship statements
- V. Acknowledgements/Podziękowania
- VI. Supplements

I. Streszczenie

Pulsy zasobów to epizody silnie zwiększonej dostępności zasobów w środowisku (Yang *et al.* 2008). Zjawisko to wpływa na liczne procesy ekologiczne takie jak dynamika liczebności populacji zwierząt i roślin, oddziaływania pomiędzy konsumentami i zasobami, czy przewalencję chorób w populacjach zwierząt (Ostfeld & Keesing 2000, Yang *et al.* 2008). Lata nasienne, definiowane jako nieregularna (występująca co kilka-kilkanaście lat) produkcja ogromnego opadu nasion przez populacje roślin (Kelly 1994, Crone & Rapp 2014), są przykładem takiego pulsu zasobów. Spektakularna zmienność w produkcji nasion ma miejsce u setek gatunków roślin występujących na niemal wszystkich kontynentach, a synchronizacja przestrzenna w produkcji nasion sięga tysięcy kilometrów (Koenig & Knops 1998, 2000, Kelly & Sork 2002, Crone, Miller & Sala 2009, Crone & Rapp 2014, Koenig *et al.* 2015).

Większość badań ekologicznych ignoruje wpływ pulsów zasobów wywołanych przez lata nasienne, używając średnich z kilku lat danych by wyciągać wnioski o diecie zwierząt, ich demografii czy zależnościach troficznych. Niemniej, biorąc pod uwagę wszechobecność lat nasiennych w przyrodzie, musimy zmienić naszą perspektywę postrzegania zjawisk z relatywnie niezmiennych pomiędzy latami, na silnie zmieniające się pod wpływem fluktującego środowiska (Holt 2008, Yang *et al.* 2008). Rozpoznanie fluktuującej dynamiki środowiska spowodowanej latami nasiennymi może pomóc rozwiązać wiele zagadkowych, niejednoznacznych wyników badań, w przypadku, gdy różne badania były po prostu przeprowadzone, gdy ekosystem znajdował się w innej fazie cyklu (Holt 2008, Yang *et al.* 2008). Co więcej,

zrozumienie w jaki sposób lata nasienne wpływają na funkcjonowanie ekosystemów poprawi nasze zdolności predykcyjne dotyczące różnych zjawisk ekologicznych, w tym ważnych z punktu widzenia socjoekonomicznego czy ochrony środowiska (Ostfeld & Keesing 2000, Ostfeld 2010, Yang *et al.* 2010).

Moja rozprawa doktorska składa się z czterech prac badawczych opisujących zestaw zmian zachodzących w ekosystemach, w których lata nasienne wywołują silne fluktuacje dostępności zasobów (Bogdziewicz *et al.* 2016*a,b,c,d*). W pierwszym rozdziale przedstawiam wyniki meta-analizy badań wpływu lat nasiennych na populacje kręgowców. Lata nasienne to zjawisko matematycznie chaotyczne, a więc niemal niemożliwe do przewidzenia (Crone *et al.* 2005, Crone & Rapp 2014, Pearse *et al.* 2016). Utrudnia to prowadzenie badań wpływu tego pulsu zasobów na populacje zwierząt i w wielu wypadkach informacje na temat efektu lat nasiennych pojawiają się w pracach naukowych przeprowadzonych w innym celu. W związku z tym, by opisać badane zjawisko jak najszerzej, opracowałem alternatywną metodę wyszukiwania prac badawczych opisujących efekty lat nasiennych na zwierzęta. Poza tradycyjnym przeszukiwaniem baz danych, przeprowadziłem też skanowanie pełnych tekstów wszystkich artykułów badawczych opublikowanych w wybranych czasopismach (by zidentyfikować badania, które opisują efekty lat nasiennych mimo, że nie zostały w tym celu zaprojektowane). Metoda ta pozwoliła mi niemal potroić liczbę artykułów w bazie danych (z 67 do 186). Wyniki wskazały, że efekty lat nasiennych są mocno zróżnicowane taksonomicznie (praca podsumowuje wpływ lat nasienych na 55 gatunków ssaków i 67 gatunków ptaków). Dane wskazują, między innymi, na równie duży wpływ lat nasiennych na ptaki, jak na małe ssaki. Niemniej, do tej pory to

gryzonie były głównym przedmiotem badań, a nasza wiedza o bezpośrednim wpływie lat nasiennych na populacje ptaków jest znikoma. Zrozumienie roli lat nasiennych dla dynamiki populacji ptaków może być więc owocnym kierunkiem przyszłych badań.

Zebrana baza danych posłużyła do przetestowania zestawu hipotez opisujących relacje pomiędzy cechami historii naturalnej zwierząt, a sposobem w jaki lata nasienne wpływają na ich populacje (hipotezy sformułowane we wcześniejszych pracach przeglądowych: Ostfeld & Keesing 2000, Yang *et al.* 2010). Analiza pokazała silną zależność pomiędzy wielkością miotu (zastosowaną jako wskaźnik tempa życia) oraz wielkością ciała (użyta jako wskaźnik mobilności) ssaków, a sposobem, w jaki lata nasienne wpływają na ich populacje. W szczególności, większe ssaki agregowały się w siedliskach bogatych w nasiona, natomiast gatunki ssaków o wysokiej rozrodczości intensyfikowały reprodukcję. Jednak żadna z tych zależności nie została znaleziona w przypadku gatunków ptaków, podkreślając potrzebę intensywniejszego ich badania w kontekście lat nasiennych.

W drugim rozdziale opisałem, w jaki sposób lata nasienne wpływają na użytkowanie przestrzeni przez małe ssaki na przykładzie myszy leśnej (*Apodemus flavicollis*) (Bogdziewicz *et al.* 2016b). Dramatyczne fluktuacje liczebności gryzoni spowodowane latami nasiennymi są jednymi z najlepiej rozpoznanych efektów troficznych lat nasiennych (Ostfeld & Keesing 2000, Bogdziewicz *et al.* 2016a). Jednak większość prac badawczych skupia się na wpływie lat nasiennych na zagęszczenia gryzoni. Inne równie ważne efekty są słabiej poznane (Bogdziewicz *et al.* 2016a). Dlatego zbadałem, w jaki sposób fluktuacje liczebności myszy leśnej spowodowane przez lata nasienne buka (*Fagus sylvatica*) wpływają na użytkowanie

przeestrzeni przez gryzonie. Oryginalność tych badań leży głównie w użyciu nowej metody obliczeniowej: modeli typu CMR (capture – mark – recapture) z komponentem przestrzennym. Modele te pozwalają na rozdzielenie wpływu zagęszczenia populacji na użytkowanie przestrzeni przez zwierzęta od wpływu innych zmiennych (np. dostępności pokarmu). Kwestia kowariancji pomiędzy zagęszczeniem populacji i innymi zmiennymi, a więc i trudność w rozdzieleniu tych efektów, jest nierozłącznym problemem w tego typu badaniach (Efford *et al.* 2016).

Do tej pory zakładano, że wzrost liczebności populacji spowodowany przez lata nasienne zmniejsza wielkość terytoriów ssaków (Lacher & Mares 1996, Mazurkiewicz & Rajska-Jurgiel 1998, Stradiotto *et al.* 2009, Auger *et al.* 2016). Jednakże, w poszczególnych fazach cyklu populacji generowanego przez lata nasienne, inne zmienne (np. struktura genetyczna populacji) także mogą fluktuować, powodując zmiany w zależności pomiędzy zagęszczeniem populacji a użytkowaniem przestrzeni. Może to mieć ważne konsekwencje dla dynamiki populacji, gdyż współdzielenie przestrzeni zapewne wpływa na intensywność oddziaływań konkurencyjnych czy transmisję chorób pomiędzy osobnikami. Wyniki pracy wskazują, że zmiany w zagęszczeniu gryzoni wywołane przez lata nasienne nie wystarczą, by wytłumaczyć wariację w użytkowaniu przestrzeni przez gryzonie pomiędzy latami nasiennymi i nienasiennymi. W rozdziale drugim dyskutuję możliwe czynniki, które mogą być odpowiedzialne za zmiany w tej zależności na różnych etapach cyklu populacji zwierząt.

W trzecim rozdziale opisuję wpływ lat nasiennych dębu na ryzyko zarażenia boreliozą u ludzi (Bogdziewicz *et al.* 2016c). Połączenie pomiędzy latami nasiennymi

a ryzykiem boreliozy zostało odnalezione i jest od tamtej pory intensywnie badane we wschodnich Stanach Zjednoczonych przez grupę badawczą Richarda Ostfelda (wyniki podsumowane w Ostfeld 2010). Badacze odkryli, że dramatyczny wzrost liczebności gryzoni spowodowany przez lata nasienne zwiększa liczebność larw kleszczy przenoszących bakterię *Borrelia burgdorferi* w dwa lata po roku nasiennym. Co zaskakujące, badania te nigdy nie zostały powtórzone w innych ekosystemach. Zebrałem dane o opadzie nasion żołądź w Polsce, liczbie przypadków boreliozy u ludzi, oraz dane z Google Trends o liczbie wyszukiwań słów kluczowych związanych z latami nasiennymi i boreliozą w przeglądarce Google (np. kleszcz, borelioza). Wyniki sugerują, że łańcuch wydarzeń łączących lata nasienne z boreliozą odkryty w USA ma miejsce również w Europie. Wskazuje to na tanie i efektywne narzędzie, które może posłużyć do przewidywania zwiększonego ryzyka choroby.

W czwartym rozdziale przedstawiam wyniki badań opisujących wpływ globalnych zmian na ekologię reprodukcji drzew, u których występują lata nasienne. Liczne badania wskazują, że globalne zmiany (takie jak ocieplenie klimatu czy zwiększające się stężenie azotu organicznego w środowisku) powodują wzrost liczby nasion produkowanych przez rośliny (np. McKone *et al.* 1998, Richardson *et al.* 2005, Overgaard *et al.* 2007, Buechling *et al.* 2016). Jednak do tej pory nie było jasne czy przekłada się to na intensywniejsze odnowienie populacji roślin (McKone *et al.* 1998). Zebrałem więc dane obserwacyjne i eksperymentalne, by oszacować wpływ chronicznej depozycji azotu organicznego na reprodukcję dębu czerwonego (*Quercus rubra*). Poza zbadaniem wpływu azotu na produkcję żołądź, przetestowałem również jego pośredni wpływ na reprodukcję dębu, wywierany poprzez zmiany w

oddziaływaniach dębu z jego najważniejszymi konsumentami nasion (chrząszczami *Curculio* sp.) oraz roznosicielami nasion (gryzonie). Wreszcie, sprawdziłem wpływ depozycji azotu na kiełkowanie żołądzi.

Okazało się, że chroniczna depozycja azotu powoduje nawet 9-krotne zwiększenie liczby nasion produkowanych przez dęby. Jednocześnie jednak nawożenie azotem spowodowało zwiększenie konsumpcji nasion przez owady, zmniejszyło wynoszenie i chowanie nasion dębu przez gryzonie, a także zmniejszyło prawdopodobieństwo kiełkowania żołądzi. Zwiększenie proporcji nasion zjadanych przez owady jest szczególnie warte podkreślenia, gdyż może oznaczać, że globalne zmiany, które prowadzą do zwiększenia liczby nasion produkowanych przez rośliny zakłócają mechanizm nasycenia konsumentów (jeden z głównych mechanizmów selekcyjnych lat nasiennych, patrz np. Pearse *et al.* 2016). Wielu badaczy zajmujących się badaniem produkcji nasion w zmieniającym się środowisku ostrzegało, że bezpośrednio, pozytywne efekty globalnych zmian mogą zaniknąć, jeżeli oddziaływania roślin z konsumentami również ulegają modyfikacjom (McKone *et al.* 1998, Richardson *et al.* 2005, Overgaard *et al.* 2007, Pearse *et al.* 2014, Koenig *et al.* 2015). W szczególności naukowcy obawiali się, że wzrost produkcji nasion w latach nienasiennych może zakłócić regulację liczebności populacji konsumentów. Moje wyniki wskazują, że tak rzeczywiście jest.

Połączenie różnych efektów wpływu depozycji azotu na dęby zniwelowało bezpośredni, pozytywny efekt zwiększonej produkcji nasion. Wyniki te podkreślają, że badanie oddziaływań biotycznych jest niezbędne dla pełnego zrozumienia wpływu globalnych zmian na zespoły roślin. Depozycja organicznego azotu w środowisku ma

miejsce w wielu ekosystemach i cały czas się powiększa (Galloway *et al.* 2004, 2008).

Podobne efekty mogą więc mieć miejsce w innych systemach, prowadząc do zmian w zespołach drzew.

II. Summary

Resource pulses are large-magnitude, low frequency, and short duration events of increased resource availability (Yang *et al.* 2008). Pulsed productivity affects multiple ecosystem processes, including dynamics of populations, interactions between consumers and resources, top-down and bottom-up effects in food webs, and disease prevalence (Ostfeld & Keesing 2000, Yang *et al.* 2008). Mast seeding, defined as the intermittent production of a large seed crop by a population of plants (Kelly 1994, Crone & Rapp 2014), is a resource pulse of high magnitude and worldwide occurrence (Ostfeld & Keesing 2000, Yang *et al.* 2010). Examples of spectacular variation in seed production come from all continents except Antarctica and synchronization in pulse release may extend up to thousands of kilometers (Koenig & Knops 1998, 2000, Kelly & Sork 2002, Crone, Miller & Sala 2009, Crone & Rapp 2014, Koenig *et al.* 2015).

The majority of wildlife population studies implicitly ignore effects of mast resource pulses on ecosystem processes, by using one or two years of data to make inferences on animal diets, demography, and trophic relationships. However, to the extent that wildlife population dynamics are driven by responses to pulsed resources, we need to change our perspective from one of relatively uniform conditions among years, to one of dynamic responses to a strongly fluctuating environment (Holt 2008, Yang *et al.* 2008). Recognizing the masting-driven transient dynamics of ecosystems might help resolve numerous issues of apparently conflicting and inconclusive study results, when different studies might simply happen to be conducted at different state of the ecosystem cycle (Holt 2008, Yang *et al.* 2008). Furthermore, since masting is an inherent trait of numerous ecosystems, recognizing how it affects ecosystem

functioning will increase our predictive abilities of different ecological phenomena, including those of conservation and socio-economical concern (Ostfeld & Keesing 2000, Ostfeld 2010, Yang *et al.* 2010).

In my PhD thesis I have conducted four case studies examining range of masting-driven changes in species interactions (Bogdziewicz *et al.* 2016*a,b,c,d*). In the first chapter I have conducted the meta-analysis of masting effects on vertebrates populations. Masting dynamics is largely chaotic and thus, it is difficult to trace and study (Crone *et al.* 2005, Crone & Rapp 2014, Bogdziewicz *et al.* 2016*a*, Pearse *et al.* 2016). Therefore, in order to capture as large picture of masting effects as possible, I have developed an alternative method of identifying studies of interest. In addition to traditional search of online databases, I have conducted the full-text search of all articles published in selected journals (in order to capture studies that found effects of mast seeding despite not being designed to study it). This method allowed me to almost triple the number of articles in the database (from 67 to 186). The results demonstrated that the effects of masting are more taxonomically diverse than past reviews widely recognized, and included responses of 55 species of mammals and 67 species of birds (belonging to 14 orders and 42 families). Based on this dataset, it is clear that birds are as responsive to masting as rodents. Yet, rodents received much more research attention, and our knowledge of direct effects of masting on birds is scarce. This suggests that studies explicitly examining the effects of masting on bird populations might provide a fruitful avenue for future research.

Furthermore, I used this large sample of species responses to test a hypothesis that species life history traits influence the type of response to masting (hypothesis

derived from past reviews: Ostfeld & Keesing, and Yang *et al.* 2010). I have found that the type of response to mast seeding of mammals is strongly related to the species litter size (as a proxy of the pace of life) and body mass (as a proxy of mobility). In particular, larger mammals are more likely to aggregate in mast-rich habitats, while mammals of higher litter size are more likely to respond to masting through increased reproduction. In contrast, none of these relationships was found for birds. This further emphasizes that mast effects of birds need more research.

In the second chapter, I described how mast seeding affects space use of the yellow-necked mice (*Apodemus flavicollis*) (Bogdziewicz *et al.* 2016b). Large fluctuations in rodent abundance caused by mast seeding are one of the best-recognized wildlife responses to masting (Ostfeld & Keesing 2000, Bogdziewicz *et al.* 2016a). However, the vast majority of work concerns masting effects on rodent reproduction or density. Other effects, despite their potential importance, received much smaller attention (Bogdziewicz *et al.* 2016a). Thus, I have used fluctuations in the yellow-necked mouse abundance to examine how mast seeding affects space use of rodents. The fluctuations were induced by European beech (*Fagus sylvatica*) masting. The novel feature of the study is the use of spatially-explicit capture recapture models that allow separation of the effect of density on animal space use from other factors (e.g. food availability). The problem of covariation between density and other factors, and thus the issue of separating those, was the inherent obstacle of numerous past studies (Efford *et al.* 2016).

The general assumption is that the masting-mediated increase in population density decreases mammals' home range size (Lacher & Mares 1996, Mazurkiewicz &

Rajska-Jurgiel 1998, Stradiotto *et al.* 2009, Auger *at al.* 2016). However, at the distinct phases of the population cycle generated by masting, other factors (e.g. kin structure) might change as well, leading to variation in the relationship between rodent density and spatial behavior. Such effects could alter the density-home range area relationship with potential consequences for population dynamics, as differences in space sharing are likely to translate into changes in competition for resources or disease transmission. I have found that the mast-induced effects of density on mice space use are not sufficient to explain the variance in space use of rodents among mast and non-mast years. In the Chapter 2 I discuss the possible factors that might be responsible for the relationships between density and space use in different phases of mast-induced population cycle.

In the third chapter I outline the impact of oaks mast seeding on the Lyme disease risk in humans (Bogdziewicz *et al.* 2016c). The connection between acorn masting and Lyme borreliosis risk was found and intensively studied in Eastern USA by the lab of Richard Ostfeld in 1990s (summarized in Ostfeld 2010). They have found that the dramatic increase in rodent abundance caused by oak masting boost the abundance of *Borrelia burgdorferi* spirochete infested ticks two years after masting. Surprisingly, however, this connection has never been studied in other systems. I have collected the Poland-wide data on acorns crop, Lyme disease cases, and Google Trends data on human cyber-behavior, i.e. the number of search terms for “kleszcz” (tick), and “borelioza” (Lyme disease) each year. My results suggest that the ecological chain reactions found in temperate USA operates also in temperate Europe. This promises a cheap and efficient way of predicting the risk of Lyme disease.

In the fourth chapter I describe how anthropogenic environmental changes affects reproductive ecology of masting trees. Numerous studies inform that anthropogenic global changes (e.g. global warming, nitrogen deposition) drive increases in plant seed production (e.g. McKone *et al.* 1998, Richardson *et al.* 2005, Overgaard *et al.* 2007, Buechling *et al.* 2016). However, it is not clear whether this increase translates into higher plant recruitment (McKone *et al.* 1998). To test this, I have combined observational data and field experiments to estimate the net effect of nitrogen addition on red oak (*Quercus rubra*) reproduction. In addition to evaluating the impact of N-addition on acorn production, I have also examined the indirect effects of fertilization on biotic interactions between oaks and their most important seed predators (weevils, *Curculio* sp.) and seed dispersers (rodents), and assessed germination potential of acorns produced by N-fertilized oaks. I found that nitrogen fertilization increases the production of acorns by oaks up to 9-fold. Simultaneously, however, it increased seed predation by weevils, decreased seed caching by rodents, and lowered the probability of acorn germination. The increase in weevil predation is particularly worth highlighting because it might mean that global changes that drive increase in seed production in masting plants also disrupt predator satiation. Many researchers that studied patterns of seed production in masting plants in changing environment warned that the direct positive effects of global changes might disappear if biotic interactions of plants are also altered (McKone *et al.* 1998, Richardson *et al.* 2005, Overgaard *et al.* 2007, Pearse *et al.* 2014, Koenig *et al.* 2015). In particular, increased seed production in non-mast years might disrupt the regulation of seed predators. My results provide evidence that this might be the case.

Combined effects of chronic nitrogen fertilization trumped the positive, nitrogen-mediated effect of increased seed production on oak reproduction. These results stress the importance of considering biotic interactions when evaluating the effects of global changes on plant communities. Nitrogen deposition in the environment is ubiquitous and accelerating (Galloway *et al.* 2004, 2008). Thus, similar effects as found in our model system might operate in others, resulting in alternations of tree communities.

Literatura / Literature

Auger J, Meyer SE, Jenkins SH (2016) A mast-seeding desert shrub regulates population dynamics and behavior of its heteromyid dispersers. *Ecology and Evolution* 6:2275-2296.

Bogdziewicz, M., Zwolak, R., & Crone, E. E. (2016a) How do vertebrates respond to mast seeding? *Oikos* 125:300-307.

Bogdziewicz, M., Zwolak, R., Redosh, L., Rychlik, L., & Crone, E.E. (2016b) Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology and Evolution*, DOI: 10.1002/ece3.2513

Bogdziewicz, M., & Szymkowiak, J. (2016c) Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe. *Basic and Applied Ecology*, 17:300-307.

Bogdziewicz, M., Crone, E. E., Steele, M. A., & Zwolak, R. (2016d) Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, DOI: 10.1111/1365-2745.12673

- Buechling, A., Martin, P.H., Canham, C.D., Shepperd, W.D., & Battaglia, M.A. (2016) Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology*, 104, 1051–1062.
- Crone, E. E., Polansky, L., & Lesica, P. (2005) Empirical Models of Pollen Limitation, Resource Acquisition, and Mast Seeding by a Bee-Pollinated Wildflower. *The American Naturalist*, 166:396-408.
- Crone, E. E., Miller, E., & Sala, A. (2009) How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters*, 12:1119-1126.
- Crone, E. E., & Rapp, J. M. (2014) Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, 1322:21-34.
- Efford, M. G., Dawson, D. K., Jhala, Y. V., & Qureshi, Q. (2016) Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography*, 39:676-688.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P. et al. (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry*, 70:153–226.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, 320:889–892.
- Holt, R. D. (2008) Theoretical perspectives on resource pulses. *Ecology* 89:671–681.
- Lacher, T.E. & Mares, M.A. (1996) Availability of resources and use of space in eastern chipmunks, *Tamias striatus*. *Journal of Mammalogy* 77:833-849.

- Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, 9:465-470.
- Kelly, D. & Sork, V. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, 33:427–447.
- Koenig, W. D. & Knops, J. M. (1998) Scale of mast-seeding and tree-ring growth. *Nature* 396: 225–226
- Koenig, W. D. & Knops, J. M. (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist* 155:59–69.
- Koenig, W.D., Knops, J.M., Carmen, W.J. & Pearse, I.S. (2015) What drives masting? The phenological synchrony hypothesis. *Ecology*, 96:184–192.
- McKone, M.J., Kelly, D. & Lee, W.G. (1998) Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology*, 4:591–596.
- Mazurkiewicz, M., Rajska-Jurgiel, E. (1998) Spatial behaviour and population dynamics of woodland rodents. *Acta Theriologica* 43:137-162.
- Ostfeld, R. S., & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15:232-237.
- Ostfeld, R.S. (2010) *Lyme disease: the ecology of a complex system*. OUP USA.
- Pearse, I. S., Koenig, W. D., & Knops, J. M. (2014) Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos*, 123:179-184.
- Overgaard, R., Gemmel, P. & Karlsson, M. (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry*, 80:555–565.

Pearse, I. S., Koenig, W. D., & Kelly, D. (2016) Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, in press, DOI: 10.1111/nph.14114

Richardson, S.J., Allen, R.B., Whitehead, D., Carswell, F.E., Ruscoe, W.A. & Platt, K.H. (2005) Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology*, 86:972–981.

Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., Rizzoli, A. (2009) Spatial organization of the yellow-necked mouse: effects of density and resource availability. *Journal of Mammalogy* 90:704-714.

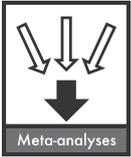
Yang, L. H., Bastow, J. L., Spence, K. O., & Wright, A. N. (2008) What can we learn from resource pulses. *Ecology*, 89:621-634.

Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N., & Spence, K. O. (2010) A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs*, 80: 125-151.

III. Doctoral dissertation

LIST OF ORIGINAL PUBLICATIONS

1. Bogdziewicz M., Zwolak R., Crone E.E. 2016. How do vertebrates respond to mast seeding? *Oikos* 125:300-307
2. Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology and Evolution*, DOI: 10.1002/ece3.2513
3. Bogdziewicz M., Szymkowiak J. 2016. Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe. *Basic and Applied Ecology* 17:300-307
4. Bogdziewicz M., Crone E.E., Steele M.A., Zwolak R. 2016. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, DOI: 10.1111/1365-2745.12673



How do vertebrates respond to mast seeding?

Michał Bogdziewicz, Rafał Zwolak and Elizabeth E. Crone

M. Bogdziewicz (http://orcid.org/0000-0002-6777-9034), (micbog@amu.edu.pl), and R. Zwolak, Dept of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, PL-61-614 Poznań, Poland. MB and E. E. Crone, Dept of Biology, Tufts University, 163 Packard Ave, Medford, MA 02155, USA. EEC also at: Harvard Forest, Harvard University, Petersham, MA 01366, USA.

Mast-seeding is the synchronized and intermittent production of a large seed crop by a population of plants. The cascading effects of masting on wildlife have been well documented in granivorous rodents. Yet, the effects of mast-seeding are potentially further reaching, since a number of generalist species can take advantage of mast years. We employed a full-text search algorithm to identify all papers that discussed effects of mast-seeding on wildlife, in addition to typical searches of titles and abstracts. We aimed to evaluate the breadth of wildlife species for which mast years are thought to be important drivers. In addition, we tested three hypotheses derived from past reviews: 1) species with lower reproductive potential (lower average litter size) are more likely to show aggregative responses to mast-seeding, 2) species with lower body sizes (lower mobility) are more likely to show reproductive responses, and 3) indirect consumers of mast (predators) are more likely to show aggregative responses than direct consumers. We found 186 articles including reports of response of 122 species of vertebrates to mast-seeding. Expectations were partly confirmed: relationships 1) and 2) held for mammals, but not for birds. However, 3) direct consumers were more likely than indirect consumers to show aggregative responses. Our tests of the first two hypotheses question the generality of past predictions for taxa other than mammals. Our test of the third hypothesis suggests that responses of direct and indirect consumers might depend on the type of resource pulse. Many of the examples in our analysis come from systems in which wildlife responses to mast have been less rigorously documented than the examples in past reviews. They suggest the range of wildlife responses to mast-seeding are more taxonomically and ecologically diverse than past reviews have widely recognized and point to directions for future research.

Synthesis

Mast seeding is a pulsed resource with numerous cascading effects on wildlife. Yet, because masting is largely unpredictable, it is inherently difficult to study. We developed a full-text search algorithm to identify incidental reports as well as deliberate studies of vertebrate reactions to masting. We found that the type of response to mast seeding (reproductive or through immigration) varies predictably as a function of life history traits (litter size and body mass) in mammals, but not in birds. Our literature search also shows that responses to mast-seeding are more taxonomically and ecologically diverse than past reviews have recognized.

Resource pulses are large-magnitude, low frequency, and short duration events of increased resource availability (Yang et al. 2008). Pulsed productivity affects multiple ecosystem processes, including dynamics of populations, interactions between consumers and resources, top-down and bottom-up effects in food webs, and disease prevalence (Ostfeld and Keesing 2000, Yang et al. 2008). Mast seeding, defined as the intermittent production of a large seed crop by a population of plants (Kelly 1994, Crone and Rapp 2014), is a resource pulse of high magnitude and worldwide occurrence (Ostfeld and Keesing 2000, Yang et al. 2010). Examples of spectacular variation in seed production come from all continents except Antarctica (Kelly and Sork 2002, Espelta et al. 2008, Crone et al. 2009, Norghauer and Newbery 2010) and synchronization in pulse release may extend up to thousands of kilometers (Koenig and Knops 1998, 2000). A more

limited set of studies have documented responses of wildlife populations to mast-seeding. These case studies provide examples of impacts of mast seeding that ramify throughout communities and cut across ecosystem boundaries (Jones et al. 1998, Curran and Leighton 2000, McSchea 2000, Schmidt and Ostfeld 2003, 2008, Lobo and Millar 2013).

To date, most of these published examples of wildlife responses to mast-seeding show a similar taxonomic structure: an increase of rodents (primary consumers) was followed by response of mustelids and raptors, and eventually caused a lagged increase in predation on birds' nests (King 1983, Jędrzejewska and Jędrzejewski 1998, McShea 2000, Clotfelter et al. 2007, Schmidt et al. 2008, Zwolak et al. 2015). The majority of wildlife population studies implicitly ignore effects of mast resource pulses, by using one or two years of data to generalize animal diets, demography

and trophic relationships. One interpretation of this pattern is that mast-seeding mostly affects trophic chains that start with granivorous rodents. Alternatively, it may be that these case studies have been well developed and highly cited, but that similar cascading effects happen in other ecological systems. To the extent that wildlife population dynamics are generally driven by responses to pulsed resources, we need to change our perspective from one of relatively uniform conditions among years, to one of dynamic responses to a strongly fluctuating environment (Holt 2008, Yang et al. 2008).

In this article, we quantify the breadth and diversity of ways in which wildlife populations respond to mast-seeding, with the specific aim of capturing incidental observations of mast year effects, as well as deliberate experimental tests of how mast years affect wildlife. In order to capture these observations, we developed a literature review approach that differs from a traditional meta-analysis. Specifically, we conducted a full-text search of entire articles in a selected subset of journals and identified all studies that mentioned masting anywhere in the text. The full-text search combined two sources of data: studies that were designed to test for effects of mast-seeding, and studies that attribute aspects of wildlife performance to mast events in a post hoc or incidental manner, even if masting was not originally part of the investigation. Thus, in one sense, the study is a much broader investigation than the traditional literature search, but this breadth comes at the cost of including qualitative observations, as well as explicit tests. We contrast the studies obtained with this full-text search algorithm to a conventional search that identified papers by keywords in titles and abstracts.

In addition to describing responses to mast-seeding, we use our data set of wildlife responses to mast-seeding to evaluate three hypotheses from two past reviews of consumer responses to pulsed resources. In the first of these reviews, Ostfeld and Keesing (2000) hypothesized that species responses to mast seeding should vary predictably as a function of the rate of population response (capacity to increase reproductive output, e.g. litter size) and species mobility (Table 1). In particular, species with slow life histories (“slow” sensu Stearns 1992) are more likely to respond to masting through mobility or a diet-switching (i.e. changes in the proportion of each prey species in the diet; Ostfeld and Keesing 2000) because of their low intrinsic capacity to increase reproductive output. Similarly, species with high reproductive capacity and poor mobility should respond via reproduction (Ostfeld and Keesing 2000). In the second review, Yang et al. (2010) found that the numerical increase

in response to pulsed resources was larger for aggregative responses than reproductive ones. Aggregation was defined as a mechanism of numerical recruitment driven by the immigration of consumers from surrounding populations (Yang et al. 2010). Frequent occurrence of the aggregative or combined (aggregative and reproductive) response was hypothesized to be the cause of particularly strong numerical increases characterizing consumers from higher trophic levels (Yang et al. 2010).

We evaluate the three hypotheses outlined in the two previous reviews as follows: 1) to evaluate the hypothesis that aggregative or diet-switching responses are more likely to occur in species with slow life history and/or high mobility, we obtained data on average litter (or clutch) size and average body mass for species in our study. Litter size is tightly linked to life history (Millar and Zammuto 1983, Heppell et al. 2000, Sæther and Bakke 2000) and has been used previously as an indicator of life history syndromes (Cardillo et al. 2003). Similarly, body mass has repeatedly been shown to correlate strongly with mobility in both birds and mammals, and has been successfully used as a surrogate of mobility in previous studies (Schoener 1968, Haskell et al. 2002, Carbone et al. 2005, Ottaviani et al. 2006, Thornton et al. 2011). We then tested whether the probability of aggregative and diet-switching responses is higher in species with lower average litter size and/or higher body mass. 2) To evaluate the hypothesis that reproductive response is more likely to occur in species with low mobility and/or fast life history, we tested whether the probability of species showing reproductive responses decreases with body mass and increases with litter size. 3) Finally, we compiled data on the trophic status of each species, in relation to mast seeding (granivore, consumer of granivores, etc). We tested whether indirect responses to masting, i.e. those at higher trophic levels, are more likely to be aggregative than reproductive.

Because of their irregular and unpredictable nature, effects of mast-seeding and other pulsed resources are inherently difficult to study. Our approach of finding and analyzing observations of wildlife responses to mast-seeding sheds new light on a relatively intractable phenomenon. Of course, the incidental observations are less rigorous evidence for how vertebrates respond to mast-seeding than the experimental tests. We see the analysis of these data as a valuable way to quantify our collective knowledge of natural history, and identify hypotheses that could be tested more rigorously.

Material and methods

Data base construction

We built two data bases, one using traditional literature search methods (hereafter traditional search or ‘TS’), and the other using full-text search. In the first, we searched ISI Web of Science and Scopus databases for peer-reviewed studies that examined the effects of mast seeding on wildlife using keyword search (*mast** AND *bird** OR *mammal** OR *rodent** OR *passer** OR *ungulat** OR *carniv** OR *animal** OR *wildlife** OR *ave** OR *omniv** OR *herbiv**

Table 1. Predictions derived from Ostfeld and Keesing (2000) review article describing how probability of vertebrate responses to mast seeding should vary predictably with their reproductive output (here, litter size) and mobility (here, body mass). All relationships held, but only for mammals, not for birds. See main text for details.

Predictor: \ Response:	Aggregation and/or diet switching	Increase in reproductive output
Species average litter/clutch size	negative relationship	positive relationship
Species average body mass	positive relationship	negative relationship

OR *artiod** AND *acorn** OR *seed**). In the second, we downloaded all articles published in *Ecology*, *Journal of Animal Ecology*, *Journal of Wildlife Management*, *Oikos*, *The Auk* and *Journal of Mammalogy* between January 1990 (or January 1997 in the case of *Ecology*) and September 2013. The time range of articles downloaded from *Ecology* was narrower because volumes published before 1997 did not have pdf-files available to download from ESA website. Next, we screened all downloaded articles for the term ‘mast*’ appearing anywhere in the text. The search was done using the freeware application PDF-XChange Viewer ver. 2.5. We chose this set of ~20 000 articles as representative of ecologists studying wildlife from ecological and conservation/management perspectives. We read articles that included the mast* term and divided them into studies designed to investigate the effects of mast seeding (hereafter targeted studies: ‘FT’ studies, for ‘full text, targeted’) and studies where effects of masting were found incidentally (hereafter non-targeted studies: ‘NT’ studies). We categorized studies with predictions on the effects of masting in the introduction section and studies where research design explicitly incorporated masting as FT studies. We categorized articles in which potential mast effects were mentioned in discussion as a possible explanation of results as NT studies. In general, NT studies were articles in which authors attributed wildlife responses to mast seeding without formal statistical analysis (e.g. high survival in a given year explained by observed background mast seeding). Based on information contained in article, we scored the type of species response (see list of responses in Results) to masting. We divided these responses into three broad categories (behavioral, demographic and physiological responses).

For each study, we recorded the identity of the masting plant species, the identity of all wildlife species that responded, and whether the response was a direct or an indirect effect of masting. Direct effects included those that were directly caused by increased availability of seeds for their primary consumers and the indirect effects included those that were caused by changes in populations of primary consumers in response to mast seeding (Ostfeld and Keesing 2000). For each wildlife species, we also recorded its body mass and mean litter size. The average body masses were obtained from Project PanTHERIA, a global species-level data set of life history ecological traits (Smith et al. 2003, Lislevand et al. 2007, Jones et al. 2009). Information on the species average litter size was obtained from AnAge Database of Animal Ageing and Longevity (Tacutu et al. 2013). Data on a few species that were not available in the above mentioned databases were obtained from other peer-reviewed sources.

Statistical analysis

We tested predictions derived from Ostfeld and Keesing (2000) and Yang et al. 2010 using generalized linear mixed effects models (GLMMs) implemented via ‘lme4’ package (Bates et al. 2013), with taxonomic order of each species as a random effect. We tested the first prediction (species with lower reproductive capacity or higher mobility are more likely to respond through aggregation or diet switching) by building two models: in the first, we modeled

the probability of reporting diet switching or aggregative response as the function of average litter size, and an interaction of litter size with species class (mammals versus birds). In the second, we replaced litter size with log-transformed body mass. We tested the second prediction (species with low mobility or high reproductive capacity are more likely to show a reproductive response) using two models with reproductive response as a binary (yes/no) response variable. In the first one, we used log-transformed average body mass and the interaction of body mass with species class as explanatory variables. In the second, we replaced body mass with litter size.

We tested whether primary and secondary consumers of mast differ in the mechanism of their responses to mast with two analyses. In the first, we modeled the probability of aggregative response in relation to trophic distance; in the second, we evaluated how trophic distance influences the probability of reproductive response.

In all models we used species as the unit of replication. In other words, if at least one study reported a type of response (e.g. reproduction) for a species, that response was included as present in that species, and if a species was included in our data base but no studies had reported that type of response, that response type was scored as absent. In all models we added the number of articles reporting response of focal species as covariate to control for differences in numbers of reports on particular species. Moreover, in all above-described models we tested whether the results of hypotheses testing would differ across different search methods. To do this, in first four models (testing the hypotheses from Ostfeld and Keesing 2000) we used three-way interaction term (life history trait \times species class \times type of search method used to found evidence of species response), and in the next two models (testing the hypothesis from Yang et al. 2010) two-way interaction term (trophic distance \times search method).

We tested whether distribution of species taxonomic orders, prevalence of behavioral, demographic and physiological responses, and frequency of direct and indirect effects differed across articles found with different search methods (traditional search, targeted and non-targeted studies from alternative search) using multinomial logistic regression implemented via the ‘nnet’ package (Venables and Ripley 2002). All statistics were computed in R (<www.r-project.org>).

Results

The nature of the dataset

Our two databases included 186 articles: 67 obtained with the traditional search and 138 with the full-text search, of which 19 overlapped between data bases (Supplementary material Appendix 1 Table A1). These studies generated 426 data points (response by species combinations). Full-text search generated 298 data points: 207 assigned to the FT category (studies designed to investigate the effects of masting, 86 articles) and 91 to the NT category (effect of mast seeding that were found incidentally, 52 articles). The sum of FT and NT articles exceeds 119 because some articles that were set up to test particular mast-related hypothesis

also reported incidental findings (Noyce and Garshelis 1997, Clark et al. 2005, Jensen et al. 2012).

The majority of studies reported responses to mast-seeding of deciduous trees, mainly oaks (47% of studies, e.g. *Quercus rubra*, *Q. crispula*, *Q. serrata*, *Q. falcata*), and beech (22% of studies, *Fagus grandifolia*, *F. sylvatica*, *Nothofagus* spp.). Other deciduous species (26%) included *Acer* spp., *Carya* spp., *Castanea* spp., *Dipterocarpaceae* spp., *Fraxinus* spp. Thirteen percent of studies recorded masting effects of coniferous species (e.g. *Abies lasiocarpa*, *Juniperus* spp., *Pinus abies*, *Pinus albicaulis*, *Pinus edulis*, *Picea glauca*). Three studies included responses to bamboo masting and one to masting of *Chionochloa* grass (Wilson and Lee 2010).

Overall, 55 species of mammals and 67 species of birds, belonging to 14 orders and 42 families, were reported to respond to masting (Supplementary material Appendix 1 Table A1). Rodents were most often reported to respond to mast seeding (50% of TS articles, 44% of FT and 42% of NT articles; Supplementary material Appendix 1 Fig. A2), followed by carnivores (TS: 14%, FT: 20%, NT: 23%), Passeriformes (TS: 14%, FT: 15%, NT: 3%), Artiodactyla (TS: 6%, FT: 11%, NT: 11%) and Galliformes (TS: 5%, FT: 2%, NT: 18%). Responses of the remaining taxonomic orders (Accipitriformes, Anseriformes, Columbiformes, Piciformes, Psittaciformes, Strigiformes, Primates, Scandentia and Soricomorpha) were found in less than 5% of all reports (Supplementary material Appendix 1 Fig. A1). The distribution of taxonomic orders differed across search methods ($\chi^2 = 22.83$, DF = 8, $p = 0.004$). Taxa had similar prevalence in TS and FT articles ($\chi^2 = 3.87$, DF = 8, $p = 0.86$). However, the distribution of taxa in NT articles differed from the distribution in FT articles ($\chi^2 = 18.13$, DF = 8, $p = 0.02$), and marginally from TS articles ($\chi^2 = 13.46$, DF = 8, $p = 0.09$). Based on inspection of 95% confidence limits, this difference was driven by four significant differences among four taxonomic groups: rodents were over-represented in TS studies, passerines were under-represented in NT studies, Galliformes were over-represented in NT studies, and carnivores were more common in NT than in TS studies.

Types of responses to masting

Studies in our database reported a diversity of responses by wildlife to mast seeding (Supplementary material Appendix 1 Table A1). Demographic responses (reproduction, survival, nest success) were most often reported (TS: 28%, FT: 31%, NT: 23%; Supplementary material Appendix 1 Fig. A2), followed by changes in species abundance (TS: 32%, FT: 23%, NT: 17%). Behavioral responses to masting included changes in movement patterns (TS: 11%, FT: 13%, NT: 20%), habitat selection (TS: 1%, FT: 9%, NT: 9%), and diet (TS: 15%, FT: 8%, NT: 11%). Physiological changes induced by masting included body condition, torpor and hibernation time (TS: 8%, FT: 12%, NT: 9%). The distribution of responses did not differ between search methods ($\chi^2 = 4.44$, DF = 4, $p = 0.34$).

In addition to effects of mast seeding, we found numerous reports of consequences of mast failure (TS: 2 articles, FT: 14, NT: 6) on focal organisms. Mast failure was attributed to cause a variety of wildlife responses in categories

resembling those reported for mast seeding: reproduction, survival, nest success, abundance, immigration, body condition, diet-switching, changes in daily distance moved, and capture probability.

Hypothesis 1. Are species with lower reproductive capacity (slower life histories) more likely to respond through aggregation or diet switching?

As predicted by Ostfeld and Keesing (2000), we found a negative relationship between litter size and probability of recording aggregative or diet switching response (Fig. 1). However, this relationship held only for mammals ($z = -2.66$, $p = 0.007$), and not for birds ($z = -0.82$, $p = 0.39$). Similarly, the probability of aggregative and diet switching responses was positively related to body mass in mammals ($z = 4.41$, $p > 0.001$; Fig. 2), but not in birds ($z = -0.07$, $p = 0.94$). Reproductive response was more likely to be recorded for mammals than birds (20 mammal species, and 9 bird species with reproductive response recorded; $z = 2.20$, $p = 0.027$). The relationship between litter size and aggregative responses differed marginally with search methods ($\chi^2 = 5.22$, DF = 2, $p = 0.07$, but this effect was driven by the different magnitude of the effect size of mammals' response, which was larger in TS than NT studies (litter size effect in NT: -2.14 intercept ± 0.88 SE, TS: -0.54 ± 0.24); the direction of the relationship stayed the same. In case of body mass and aggregative/diet switching response the relationship did not differ with search methods ($\chi^2 = 1.09$, DF = 2, $p = 0.58$).

Hypothesis 2. Are smaller (less mobile) species more likely to show reproductive response?

As predicted by Ostfeld and Keesing (2000), we found a negative relationship between body size and the probability of recording species increase in reproductive investment in response to mast seeding, although this response was not statistically significant at the $p < 0.05$ level. This relationship was stronger for mammals ($z = -1.73$, $p = 0.08$;

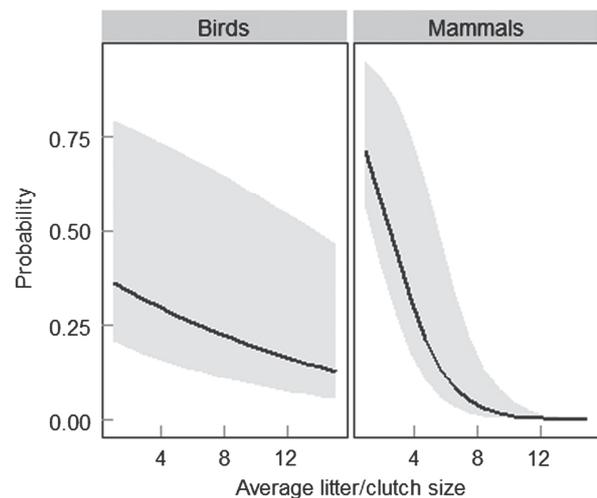


Figure 1. Generalized linear mixed model curves representing the average marginal probability of displaying aggregative or diet switching response in relation to clutch (birds) and litter (mammals) size to mast seeding. Shaded regions represent confidence intervals (95%) for the curve.

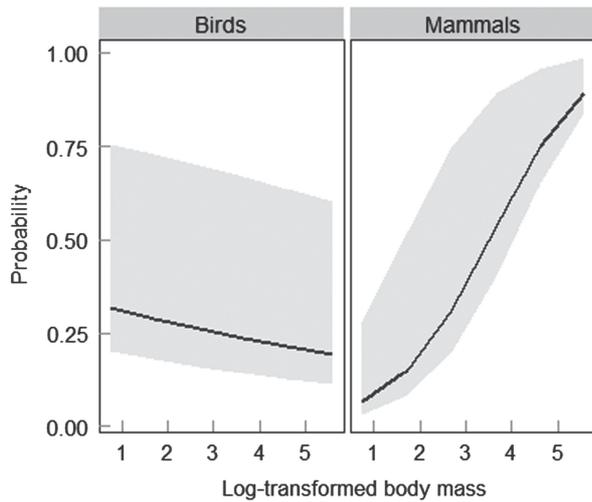


Figure 2. Generalized linear mixed model curves representing the average marginal probability of displaying aggregative or diet switching response in relation to log-transformed body mass to masting. Shaded regions represent confidence intervals (95%) for the curve.

Fig. 3), than for birds ($z = 1.40$, $p = 0.16$). Moreover, in case of birds, the non-significant relationship between body size and reproductive response was positive. The probability of recording reproductive response was positively related to litter size in mammals ($z = 3.31$, $p > 0.001$; Fig. 4), but not in birds ($z = -0.27$, $p = 0.78$). Aggregation and diet switching was equally likely to be recorded for mammals and birds (26 mammal, 22 bird species with focal response; $z = 0.82$, $p = 0.41$). The outcome of hypothesis testing did not differ across search methods (test with body mass: $\chi^2 = 0.99$, $DF = 2$, $p = 0.61$; test with litter size: $\chi^2 = 0.06$, $DF = 2$, $p = 0.97$).

Hypothesis 3. Are indirect consumers more likely to respond to mast seeding through aggregation?

Contrary to expectations, aggregative response was more likely to be associated with direct than indirect consumers

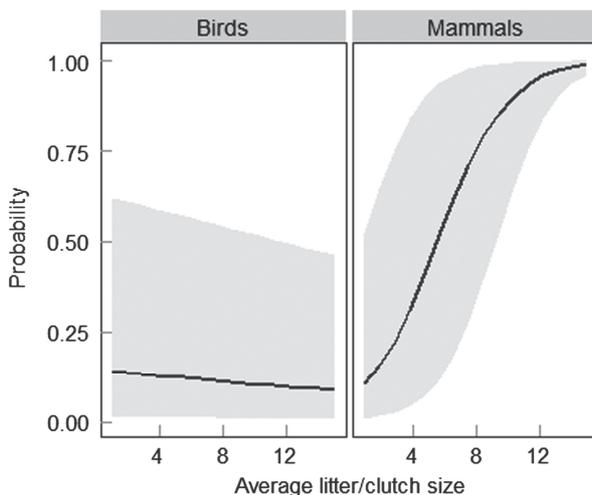


Figure 3. Generalized linear mixed model curves representing the average marginal probability of displaying reproductive response in relation to clutch (birds) and litter (mammals) size to mast seeding. Shaded regions represent confidence intervals (95%) for the curve.

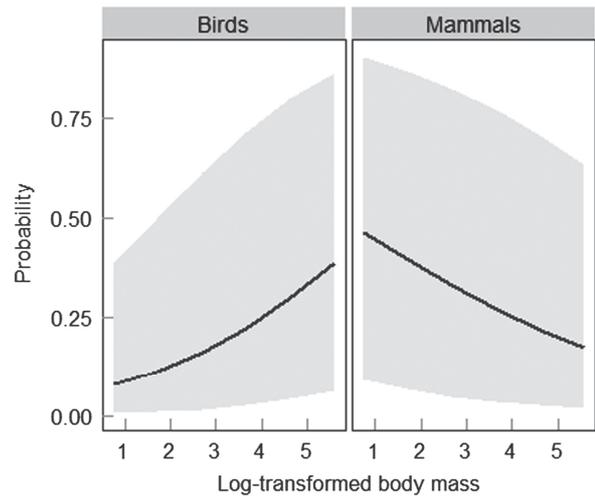


Figure 4. Generalized linear mixed model curves representing the average marginal probability of displaying reproductive response in relation to log-transformed body mass to masting. Shaded regions represent confidence intervals (95%) for the curve.

($z = 2.22$, $p = 0.026$). The probability of reproductive responses did not differ between direct and indirect consumers ($z = 0.68$, $p = 0.49$). The outcome did not differ across search methods (aggregative response: $\chi^2 = 0.01$, $DF = 2$, $p = 0.99$; reproduction: $\chi^2 = 1.19$, $DF = 2$, $p = 0.55$). Generally, aggregative responses were recorded for 23 species and reproductive responses for 29 species. Only five species were recorded to respond jointly by these two mechanisms: the bearded pig *Sus barbatus*, the black bear *Ursus americanus*, crested partridge *Rollulus rouloul*, the great tit *Parus major* and the jungle fowl *Lophura* spp.

Discussion

Overall, we found reports of response to mast seeding for 122 species of vertebrates belonging to 14 orders and 43 families. In the studies identified through the full-text literature search, responses to mast were not strongly biased toward granivorous rodents and their food webs. In fact, many species respond to masting, including passerines, large omnivores such as bears, ungulates and primates, and generalist birds such as mallards and pheasants (Supplementary material Appendix 1). Moreover, the diversity of responses shown by passerines expanded beyond nest success and resembled those reported for rodents, making these two groups equally responsive to mast seeding.

High reproductive capacity and low mobility are tightly linked with reproductive response in mammals, but not in birds. In small mammals with high reproductive capacity (e.g. rodents), mast seeding effects on reproductive output are well-appreciated and described: masting increases the number of juveniles per female (Bergeron et al. 2011), increases proportion of yearling and adult breeders (Boutin et al. 2006), induces winter breeding (Pucek et al. 1993), and has long-lasting positive effects on reproductive success of females born in mast year (Descamps et al. 2008). In contrast, masting effects on reproductive ecology of birds are much less known and are rarely the focus of research.

The best described effects on birds' recruitment are indirect via a mast-rodent-predators-nest success link: i.e. changes in nest predation (McShea 2000, Schmidt and Ostfeld 2008), and brood size of birds of prey (Jędrzejewski et al. 1996). Our literature review shows that birds also respond directly to mast-seeding. For example, clutch size tends to be higher in mast years in Galliformes (Curran and Leighton 2000, Devers et al. 2007). In addition, in great tits mast failure decreases recruitment (Grøtan et al. 2009), and influences fledging production (Bouwhuis et al. 2010). Overall, increase in abundance is the most often reported response to mast seeding for both birds and mammals. These studies of reproductive responses in birds did not show up in the traditional literature search because 'mast' was not among the key words. Thus, we suggest that more explicit studies of the role of mast seeding for birds' reproductive ecology would be a useful area for future research.

The lack of association between body size and the aggregative response/diet switching in birds might be the result of overall higher mobility of birds than mammals, which may allow them to move freely among habitats (Fraser and Stutchbury 2004, Thornton et al. 2011). Indeed, among mammals, large-scale movement in response to mast was reported for bears and ungulates, while, among birds, movement between habitats was reported for species as large as turkeys (average body mass 7400 g) and as small as red-breasted nuthatches (11 g). In contrast to aggregative responses, diet switching involved a much higher diversity of mammal species, indicating that potential for large-scale movement between habitats drove the relationship between body size and diet switching. The potential for movement in relation to mast-seeding could be incorporated into conservation plans of large mammals. For example, attraction to mast can move focal species outside protection areas and decrease their survival (Beringer et al. 1998). It can also induce predictable fluctuations in herbivore pressure across landscapes as large mammals such as ungulates, aggregate in mast-rich areas.

In their review, Yang et al. (2010) found that indirect responses to resource pulses tend to be larger in magnitude than direct ones. They suggested that a higher likelihood of aggregative or combined response in indirect consumers might be responsible for this pattern, since these two mechanisms created the most powerful increases. We found only five species with such a combined response to mast seeding. Moreover, contrary to the expectation, the likelihood of aggregative response was higher in direct than in indirect consumers. This pattern was mostly driven by generalist birds that aggregate in mast-rich habitats (Koenig 2001, Koenig and Knops 2001, Sæther et al. 2007). Yang et al. (2010) included only one example of changes in bird abundance, thus the difference in results might be related to different taxa included in its and our analyses. Alternatively, our findings might imply that wildlife responses to mast seeding differ from responses to pulsed resources in general.

Our full-text search pointed wildlife responses that are often attributed to mast seeding, but have to date rarely been the focus of research. For example, many NT studies attribute changes in habitat selection to mast seeding. Mechanisms include both aggregation toward mast-resources, and indirect responses to changes in population density. Few targeted studies (TS) have explored how mast-seeding

changes habitat selection (but see e.g. Kilpatrick et al. 2011). Therefore, researchers interested in habitat selection should be particularly aware that the selected habitats are likely to vary through time. Importantly, ignoring mast effects could lead to false interpretation of results: e.g. habitat could be wrongly assigned as a sink while the low survival in population is caused by mast failure (Mahon and Martin 2006).

We also found a variety of effects of mast failure on wildlife. Such a variety of phenomena explained by mast failure suggest that events of resource scarcity may have similarly broad effects on ecosystems as mast itself; especially in ecosystems where some seed production usually happens, e.g. in North American hardwood forests (McShea 2000, Kelly et al. 2008). We speculate that, in systems where abundant resources are common, occasional resource troughs could contribute to population and community dynamics, with equally far-reaching effects to resource pulses. However, the theoretical implications of famine pulses in food webs have been largely overlooked (but see Sears et al. 2004). Thus, it is unclear if they act simply as mast years à rebours or whether they have their own, unique effects.

One limitation of our review is that it is biased towards temperate hardwood forests. This was not intended, but is logical in hindsight based on the set of journals that we chose for full-text search. Inclusion of journals specializing in tropical or Southern Hemisphere would be an interesting direction for future research. We suspect that the bias towards hardwood forests reflects researcher bias, as this pattern was evident in both search methods, rather than lack of important mast-consumer interactions in conifer-dominated or grassland systems (Wilson and Lee 2010, Lobo and Millar 2013, Lobo 2014).

In conclusion, many aspects of animal ecology may be influenced by highly dynamic processes such as mast-seeding. Ecologists have long been aware of the importance of "rare" or "surprising" events (Weatherhead 1986, Doak et al. 2008, Lindenmayer et al. 2010), but these are inherently difficult to study. Our full-text approach to identify examples of responses to mast-seeding is broadly analogous to other 'big data' studies in ecology, in which we obtain low-resolution data over broad scales in space and time (Dickinson et al. 2012, Breed et al. 2013, Szymkowiak and Kuczyński 2015). As our data-processing abilities increase, and journal access increases, this approach may be a valuable way to broaden our understanding of the importance of different kinds of rare events in general.

Acknowledgements – We would like to thank Agnieszka Amborska for her invaluable help with screening articles. The work was done while RZ and MB were supported by a (Polish) National Science Centre Harmonia grant no. 2012/04/M/NZ8/00674 awarded to RZ. MB was supported by Adam Mickiewicz Univ. Foundation Scholarship awarded in 2014 and by National Science Centre grant 'Etiuda' no. 2015/16/T/NZ8/00018 for preparation of doctoral dissertation. EEC was supported by NSF DEB 10-20889 and funding from Harvard Forest.

References

Bates, D. et al. 2013. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.0-4.

- Bergeron, P. et al. 2011. Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. – *Ecology* 92: 2027–2034.
- Beringer, J. et al. 1998. The influence of a small sanctuary on survival rates of black bears in North Carolina. – *J. Wildl. Manage.* 62: 727–734.
- Boutin, S. et al. 2006. Anticipatory reproduction and population growth in seed predators. – *Science* 314: 1928–1930.
- Bouwhuis, S. et al. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. – *J. Anim. Ecol.* 79: 1251–1261.
- Breed, G. A. et al. 2013. Climate-driven changes in northeastern US butterfly communities. – *Nat. Clim. Change* 3: 142–145.
- Carbone, C. et al. 2005. How far do animals go? Determinants of day range in mammals. – *Am. Nat.* 165: 290–297.
- Cardillo, M. et al. 2003. Geographic range size, life history and rates of diversification in Australian mammals. – *J. Evol. Biol.* 16: 282–288.
- Clark, J. D. et al. 2005. Bait stations, hard mast, and black bear population growth in Great Smoky Mountains National Park. – *J. Wildl. Manage.* 69: 1633–1640.
- Clotfelter, E. D. et al. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. – *Oecologia* 154: 493–503.
- Crone, E. E. and Rapp, J. M. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. – *Ann. N. Y. Acad. Sci.* 1322: 21–34.
- Crone, E. E. et al. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. – *Ecol. Lett.* 12: 1119–1126.
- Curran, L. and Leighton, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. – *Ecol. Monogr.* 70: 101–128.
- Descamps, S. et al. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. – *J. Anim. Ecol.* 77: 305–314.
- Devers, P. K. et al. 2007. Ruffed grouse population ecology in the Appalachian region. – *Wildl. Monogr.* 168: 1–36.
- Dickinson, J. L. et al. 2012. The current state of citizen science as a tool for ecological research and public engagement. – *Front. Ecol. Environ.* 10: 291–297.
- Doak, D. F. et al. 2008. Understanding and predicting ecological dynamics: are major surprises inevitable? – *Ecology* 84: 952–961.
- Espelta, J. M. et al. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. – *Ecology* 89: 805–817.
- Fraser, G. S. and Stutchbury, B. J. 2004. Area-sensitive forest birds move extensively among forest patches. – *Biol. Conserv.* 118: 377–387.
- Grøtan, V. et al. 2009. Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations. – *J. Anim. Ecol.* 78: 447–459.
- Haskell, J. P. et al. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. – *Nature* 418: 527–530.
- Heppell, S. S. et al. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. – *Ecology* 81: 654–665.
- Holt, R. D. 2008. Theoretical perspectives on resource pulses. – *Ecology* 89: 671–681.
- Jensen, P. G. et al. 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. – *J. Wildl. Manage.* 76: 489–502.
- Jędrzejewska, B. and Jędrzejewski, W. 1998. Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. – Springer.
- Jędrzejewski, W. et al. 1996. Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). – *J. Anim. Ecol.* 65: 105–120.
- Jones, C. G. et al. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. – *Science* 279: 1023–1026.
- Jones, K. E. et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090–184. – *Ecology* 90: 2648–2648.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. – *Trends Ecol. Evol.* 9: 465–470.
- Kelly, D. and Sork, V. L. 2002. Mast seeding in perennial plants: why, how, where? – *Annu. Rev. Ecol. Syst.* 33: 427–447.
- Kelly, D. et al. 2008. An intercontinental comparison of the dynamic behavior of mast seeding communities. – *Popul. Ecol.* 50: 329–342.
- Kilpatrick, H. J. et al. 2011. Effects of landscape and land-ownership patterns on deer movements in a suburban community. – *Wildl. Soc. B.* 35: 227–234.
- Koenig, W. D. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. – *Ecology* 82: 2636–2644.
- Koenig, W. D. and Knops, J. M. 1998. Scale of mast-seeding and tree-ring growth. – *Nature* 396: 225–226.
- Koenig, W. D. and Knops, J. M. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. – *Am. Nat.* 155: 59–69.
- Koenig, W. D. and Knops, J. M. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. – *J. Anim. Ecol.* 70: 609–620.
- King, C. M. 1983. The relationships between beech (*Nothofagus* Sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. – *J. Anim. Ecol.* 52: 141–166.
- Lindenmayer, D. B. et al. 2010. Improved probability of detection of ecological “surprises”. – *Proc. Natl. Acad. Sci. USA* 107: 21957–21962.
- Lislevand, T. et al. 2007. Avian body sizes in relation to fecundity, mating system, display behavior and resource sharing. – *Ecology* 88: 1605.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: a review of the patterns, implications, and limitations of top-down and bottom-up interactions. – *For. Ecol. Manage.* 328: 45–54.
- Lobo, N. and Millar, J. S. 2013. Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. – *J. Anim. Ecol.* 82: 814–825.
- Mahon, C. L. and Martin, K. 2006. Nest survival of chickadees in managed forests: habitat, predator and year effects. – *J. Wildl. Manage.* 70: 1257–1265.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. – *Ecology* 81: 228–238.
- Millar, J. S. and Zammuto, R. M. 1983. Life histories of mammals: an analysis of life tables. – *Ecology* 64: 631–635.
- Norghauer, J. M. and Newbery, D. M. 2010. Recruitment limitation after mast-seeding in two African rain forest trees. – *Ecology* 91: 2303–2312.
- Noyce, K. V. and Garshelis, D. L. 1997. Influence of natural food abundance on black bear harvests in Minnesota. – *J. Wildl. Manage.* 61: 1067–1074.
- Ostfeld, R. S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. – *Trends Ecol. Evol.* 15: 232–237.
- Ottaviani, D. et al. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. – *J. Zool.* 269: 317–330.

- Pucek, Z. et al. 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. – *Acta Theriol.* 38: 199–232.
- Schmidt, K. A. and Ostfeld, R. S. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. – *Ecology* 84: 406–415.
- Schmidt, K. A. and Ostfeld, R. S. 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. – *Ecology* 89: 635–646.
- Schmidt, K. A. et al. 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. – *J. Anim. Ecol.* 77: 830–837.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. – *Ecology* 49: 123–141.
- Sears, A. L. W. et al. 2004. Feast and famine in food webs: the effects of pulsed productivity. – In: Polis, G. A. et al. (eds), *Food webs at the landscape level*. Chicago Univ. Press, pp. 359–386.
- Sæther, B.-E. and Bakke, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. – *Ecology* 81: 642–653.
- Sæther, B.-E. et al. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. – *J. Anim. Ecol.* 76: 315–325.
- Smith, F. A. et al. 2003. Body mass of late Quaternary mammals. – *Ecology* 84: 3403.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford Univ. Press.
- Szymkowiak, J. and Kuczyński, L. 2015. Avoiding predators in a fluctuating environment: responses of the wood warbler to pulsed resources. – *Behav. Ecol.* doi:10.1093/beheco/aru237.
- Tacutu, R. et al. 2013. Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. – *Nucleic Acids Res.* 41: D1027–D1033.
- Thornton, D. H. et al. 2011. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. – *Landscape Ecol.* 26: 7–18.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*, 4th edn. – Springer.
- Weatherhead, P. J. 1986. How unusual are unusual events? – *Am. Nat.* 128: 150–154.
- Wilson, D. J. and Lee, W. G. 2010. Primary and secondary resource pulses in an alpine ecosystem: snow tussock grass (*Chionochloa* spp.) flowering and house mouse (*Mus musculus*) populations in New Zealand. – *Wildl. Res.* 37: 89–103.
- Yang, L. H. et al. 2008. What can we learn from resource pulses. – *Ecology* 89: 621–634.
- Yang, L. H. et al. 2010. A meta-analysis of resource pulse–consumer interactions. – *Ecol. Monogr.* 80: 125–151.
- Zwolak, R. et al. 2015. Beech masting modifies the response of rodents to forest management. – *For. Ecol. Manage.* doi: 10.1016/j.foreco.2015.10.017.

Supplementary material (available online as Appendix oik-03012 at <www.oikosjournal.org/appendix/oik-03012>). Appendix 1.

Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle

Michał Bogdziewicz¹ | Rafał Zwolak¹ | Lauren Redosh² | Leszek Rychlik¹ | Elizabeth E. Crone²

¹Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

²Department of Biology, Tufts University, Medford, MA, USA

Correspondence

Michał Bogdziewicz, Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland.
Email: micbog@amu.edu.pl

Funding information

Polish Ministry of Science and Higher Education, Grant/Award Number: NN304391537; Polish National Science Centre, Grant/Award Number: 2012/04/M/NZ8/00674; National Science Centre, Grant/Award Number: 2015/16/T/NZ8/00018

Abstract

Home range size generally decreases with increasing population density, but testing how this relationship is influenced by other factors (e.g., food availability, kin structure) is a difficult task. We used spatially explicit capture–recapture models to examine how home range size varies with population density in the yellow-necked mouse (*Apodemus flavicollis*). The relationship between population density and home range size was studied at two distinct phases of population fluctuations induced by beech (*Fagus sylvatica*) masting: post-mast peak in abundance (first summer after mast, $n = 2$) and subsequent crash (second summer after mast, $n = 2$). We live-trapped mice from June to September to avoid the confounding effects of autumn seedfall on home range size. In accordance with general predictions, we found that home range size was negatively associated with population density. However, after controlling for the effect of density, home ranges of mice were larger in post-mast years than during the crash phase. This indicates a higher spatial overlap among neighbors in post-mast years. We suggest that the increased spatial overlap is caused by negative density-dependent dispersal that leads to high relatedness of individuals within population in the peak phase of the cycle.

KEYWORDS

density dependence, home range, mast seeding, population cycles, space use, spatially explicit capture recapture

1 | INTRODUCTION

Space use (home range) allows an animal to access resources necessary to ensure its survival and reproduction (Burt, 1943; Ostfeld, 1990), influences gene flow and interactions with other species, and thus is considered an important feature regulating population dynamics (Adams, 2001; Andreassen, Glorvigen, Rémy, & Ims, 2013; Lambin & Yoccoz, 1998; Schmidt & Ostfeld, 2003). Several factors, including population density, food availability, sex, predation, and kin structure, jointly influence individual spacing behavior (Boutin, 1990; Desy, Batzli, & Liu, 1990; Godsall, Coulson, & Malo, 2014; Kawata, 1990; McLoughlin & Ferguson, 2000; Schoepf, Schmohl, König, Pillay, & Schradin, 2015).

Population density is believed to be the primary determinant of animal space use, with home range area generally decreasing with increasing density (Adams, 2001; Efford, Dawson, Jhala, & Qureshi, 2016). Nonetheless, the relationship between density and spacing behavior is mediated by other factors leading to variation in the spatial overlap among neighboring individuals. For example, higher food availability relaxes the effects of population density on space use (Adams, 2001; Schoepf et al., 2015). Similarly, higher genetic relatedness within population leads to higher spatial overlap among individuals (Le Galliard, Gundersen, Andreassen, & Stenseth, 2006; Pilot, Dąbrowski, Jancewicz, Schtickzelle, & Gliwicz, 2010). At the same time, the increased resource sharing might negatively affect

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

individual reproductive success (Lambin & Krebs, 1993), and spatial overlap among individuals determines the rate of disease transmission (Pedersen & Greives, 2008; Proffitt, White, & Garrott, 2010). Thus, recognizing how density and other factors interact in determining the population spatial structure is crucial to understanding population dynamics (Andreassen et al., 2013). However, separating effects of density from other factors in natural populations is difficult, because different factors covary in space and time (Efford et al., 2016; Schoepf et al., 2015).

Spatially explicit capture–recapture (SECR) models provide a new tool to evaluate temporal or spatial changes in space use in relation to population density (Efford et al., 2016). In SECR models, population density (D) is estimated simultaneously with the spatial scale of detection (σ), a measure of space use (Efford, 2004). Each animal is assumed to occupy a home range center at an unknown location, and each detector (e.g., live trap) is set at known location described by Cartesian coordinates (Borchers & Efford, 2008; Efford, 2004). The detection function describes the increasing probability of detection with decreasing distance between an animal's home range center and the detector (Borchers & Efford, 2008; Efford & Fewster, 2013; Efford et al., 2016). Thus, the spatial scale of detection (σ) increases with the home range, and the parameter σ is a model-based index of home range size (Efford et al., 2016). Both parameters (D and σ) might vary among populations, and their relationship reflects the degree of overlap between individual home ranges (Efford et al., 2016). This relationship can be parameterized equivalently using k that describes the degree of overlap between home ranges ($k = \sigma\sqrt{D}$) (Efford et al., 2016).

In this work, we used SECR models to evaluate whether the relationship between population density and small mammals' space use differs at two distinct phases of the rodent population cycle: post-mast peak in abundance (first summer after masting; hereafter FSA) and subsequent crash (second summer after masting; SSA). We used yellow-necked mouse (*Apodemus flavicollis*; Figure 1) population as a model system. The fluctuations of the studied population are induced by beech (*Fagus sylvatica*) mast seeding (Zwolak, Bogdziewicz, & Rychlik, 2016), that is, the intermittent and synchronized production



FIGURE 1 Yellow-necked mouse (*Apodemus flavicollis*) is a granivorous woodland rodent common in Europe (photo by Stanisław Pagacz)

of seeds (Crone & Rapp, 2014; Kelly, 1994). Strong effects of masting on rodent population dynamics occur in a variety of ecosystems leading to several fold increases in population abundance after mast years (Bogdziewicz, Zwolak, & Crone, 2016; Ostfeld & Keesing, 2000). The general assumption is that the masting-mediated increase in population density decreases mammals' home range size (Auger, Meyer, & Jenkins, 2016; Kozakai et al., 2011; Lacher & Mares, 1996; McShea & Schwede, 1993; Stradiotto et al., 2009). However, at the distinct phases of the population cycle generated by masting, other factors (e.g., kin structure) might vary as well, leading to variation in the relationship between rodent density and spatial behavior. Such effects could alter the density–home range area relationship with potential consequences for population dynamics.

Our null hypothesis is that the effects of masting on rodent space use are solely density-mediated, that is, the relationship between density and home range area does not differ between FSA (i.e., peak of the population cycle) and SSA (subsequent crash phase of the population cycle) years. Alternatively, the relationship could differ between the phases of the population cycle, revealing more complicated effects of masting on rodent populations. The direct influence of beech seed abundance on space use of mice is ruled out, because we sampled rodent populations only during summer, when beech seeds are unavailable (they are produced in the fall and germinate or rot in the spring). Therefore, we are able to use relationships between density and home range use in FSA and SSA years to test whether changes in density are sufficient to explain changes in home range size or whether additional factors need to be invoked. Based on patterns in our data, we discuss additional factors that might be responsible for relationships between density and space use in different phases of mast-induced population cycles.

2 | METHODS

2.1 | Natural history

The yellow-necked mouse is a granivorous woodland rodent that is common in deciduous forests of central and eastern Europe. In beech forests, mice rely on spatially clumped and fluctuating resources (nuts) (Jensen, 1982; Zwolak et al., 2016), and mast seeding of beech causes strong fluctuations in the abundance of mice (Jensen, 1982; Zwolak et al., 2016). Mast of deciduous trees is the main food source of the mouse (>80% of the diet), in both mast and nonmast years (Drózdź, 1966; Selva, Hobson, Cortés-Avizanda, Zalewski, & Donázar, 2012). The post-mast increase in rodent abundance is driven by high overwinter survival and winter breeding (Jensen, 1982; Pucek, Jedrzejewski, Jedrzejewska, & Pucek, 1993). Factors affecting the post-outbreak crash in rodent numbers are less known, but low food availability, predation, and disease are likely candidates (Pedersen & Greives, 2008; Pucek et al., 1993). Females' space use is expected to be driven by food availability, and males' space use by female distribution (Ostfeld, 1990; Stradiotto et al., 2009). Thus, females are expected to maintain smaller and more exclusive territories than males (Ostfeld, 1990; Stradiotto et al., 2009).

2.2 | Study site

We trapped small mammals in Gorzowska Forest (Map S1, Appendix S1), situated in western Poland. The forest is located in temperate climate zone at an altitude of 60–80 m. Average annual precipitation equals 523 mm, and average annual temperature 8°C. Common tree species include *Fagus sylvatica*, *Quercus* spp., *Pinus sylvestris*, and *Larix decidua*. For the study, we selected eight sites solely occupied by beech trees. Distances among sites averaged 1.6 km ($SD = 0.8$ km, range: 0.4–6 km). More detailed description of study sites can be found in Zwolak et al. (2016).

2.3 | Small mammal trapping

We trapped small mammals during four years (2010–2013), in four monthly sessions (June–September). We divided the sites into two sets, and sites within each set were trapped simultaneously for five consecutive nights (i.e., 40 960 trap nights in total). At each site, we set up 8×8 trapping grids with 10-m spacing between trap stations. One wooden live trap (“dziekanówka” type, widely used in Poland, size $21 \times 8 \times 9.5$ cm) was placed at each trap station and baited with rolled oats and sunflower seeds. The traps that we used are designed for single catches, but double catches sometimes occurred. We checked traps in the morning (starting at 08:00) and in the evening (starting at 18:00). We identified captured rodents to species, determined their sex, and marked them with uniquely numbered ear tags.

2.4 | Beech nut production

We determined yearly beech seed production by counting seeds on the ground (Hilton & Packham, 1997). We sampled beech by collecting and counting all seeds in 0.25 m^2 squares (24 per site in 2009 and 12 per site in 2010–2012) centered on randomly selected trap stations. Each year, we selected the points in a stratified random manner: Each site was divided into four subplots, with six (2009) or three (2010–2012) trap stations per subplot used as sampling points. The sampling was conducted once per year in late October after seeds had fallen in mid-October.

2.5 | Spatially explicit capture–recapture models

We estimated the population density (D) by fitting models using the detection function $\lambda(d; \lambda_0, \sigma)$ that describes the decline in cumulative probability of detection λ with increasing distance d between an animal home range center and a trap (Borchers & Efford, 2008; Efford et al., 2016). The parameter λ_0 represents the probability of detecting an individual when a trap is located at its activity center. The parameter σ is the spatial scale of detection that describes the relationship between detection probability and the distance between a trap and an animal activity center, that is, a metric of home range size (Efford et al., 2016). We fitted models using the “secr” package in R (Efford, 2015). We assumed home range centers to follow a uniform Poisson process (for details see, e.g., Borchers & Efford, 2008; Efford & Fewster, 2013).

The detection function followed a half-normal curve. We used models with multicatch traps, but estimates of D and σ are robust to this kind of model misspecification (Efford, Borchers, & Byrom, 2009a). We set the spatial buffer over the grid at 100 m after checking that density estimates did not vary with increased width.

We fitted separate models to data for male and female mice because the SECR models are computationally intense and fitting the global model for the complete dataset was not feasible. In addition, we expected a priori that space use would differ between males and females, with stronger territoriality in female mice (Ostfeld, 1990). For simplicity, we used only morning catches in the analysis (these constituted >98% of total mouse captures). Model parameters (D , λ_0 , and σ) were set to be constant or varying among trapping sessions; λ_0 also included (global) behavioral difference between initial and subsequent captures (i.e., trap happy or trap shy). We allowed D , λ_0 , and σ to vary independently. Thus, we fitted 12 models for each sex representing all possible combinations of these three parameters. All models also included separate parameters for each site, that is, the most simple, “constant” model included eight estimates of λ_0 , D , and σ (one for each site). Thus, the most complicated model included 48 estimates of each parameter, one for each of 16 trapping sessions at each site. The best model was selected with the Akaike’s information criterion corrected for small sample size, AICc (Burnham & Anderson, 2002). We also present Akaike weights (w_i), which can be interpreted as the weight of evidence in favor of a particular model relatively to other considered models (Burnham & Anderson, 2002).

We also explored models with density dependence of sigma differing only between phases of the mast-induced population cycle (using the k re-parameterization of SECR, see Efford et al., 2016). However, more complicated models with σ and density differing independently with years and sites fitted data far better (according to AICc scores, presumably due to other factors that also differed among sites and years). Therefore, we fitted more complicated models to avoid biased parameter estimates and then tested whether the density versus sigma relationship is affected by masting with generalized linear mixed models. Based on the estimated D_p and σ_p , we calculated session-specific k_p and used this parameter to calculate S_{95} ($S_{95} = 6\pi k^2$), which represents an estimate of the number of individuals that occurs at any time within the area of an individual’s 95% home range limits (for details and assumptions see Efford et al., 2016).

2.6 | Generalized linear mixed models

We explored the relationship between SECR-based estimates of home range size (σ), rodent density, and mast seeding with generalized linear mixed models (GLMMs) implemented in R using “lme4” package (Bates, Maechler, Bolker, & Walker, 2015). In the first model, we tested whether rodent density differs according to masting history and between males and females. Here, we used log-transformed rodent density (D) as response variable, and mast seeding (FSA vs. SSA), sex, and two-way interaction as fixed effects. In the second model, we tested whether home ranges differ according to mast history, population density, and sex. Here, we used log-transformed σ as the response variable, and

log-transformed mouse density, mast seeding, sex, and all their two-way interactions as fixed effects. In both models, we used study site as a random effect and month as a covariate. We used Gaussian family, identity link models, and tested for statistical significance of fixed factors with Wald Type II test, implemented via the "car" package in R (Fox & Weisberg, 2011).

3 | RESULTS

Beech produced abundant seed crops in 2009 (mean \pm SD: 345 ± 80 nuts/m²) and 2011 (382 ± 83 nuts/m²). In 2010 and 2012, beech failed to produce seeds: No nuts were found on the ground or observed on the tree branches.

For both sexes, density (D) and home range size (σ) varied among trapping sessions (Table 1). In males, model assuming D and σ varying among sessions strongly outperformed all others (Δ AICc \geq 77.11). In females, the difference between this model and the second best was smaller (Δ AICc = 3.60), but the evidence ratio (w_1/w_2) for the best model versus the second was 6.03. Therefore, we estimated D and σ separately for each trapping session (for parameter estimates see Table 1 in Appendix) and input these estimates into GLMMs.

Mouse densities were higher in FSA than in SSA years (main effect of "mast," $\chi^2 = 177.19$, $p < .001$), and density of males was higher than that of females (the main effect of "sex," $\chi^2 = 5.10$, $p = .02$, Figure 2). The effect of mast seeding on rodent density did not differ between sexes (mast \times sex interaction, $\chi^2 = 0.01$, $p = .90$). In the crash phase, the average densities were estimated as 6.37 ± 5.95 (mean \pm SD) individuals/ha in males and 5.26 ± 5.33 inds/ha in females. In the peak phase, the density increased fourfold: to 27.68 ± 17.61 inds/ha in males and 22.36 ± 15.89 inds/ha in females.

As expected, home range size declined with density (main effects of density in Table 2, Figure 2). Home range size also differed between phases of the mast-induced population cycle (the main effects of "mast" in Table 2, Figure 3). After correcting for changes in density, yellow-necked mice had larger home ranges in FSA than in SSA years. Home range sizes also differed significantly between male and female mice; males had larger home ranges (the main effect of Sex in Table 2, Figure 3). We also observed a significant Mast \times Sex interaction (Table 2); home range size of female mice differed more between phases of the mast-induced population cycle than home range size of males. No other interactions were statistically significant (Table 2).

The parameter k (index of home range overlap, Efford et al., 2016) averaged among sites and months (\pm SE) was 0.54 (\pm 0.01) for females and 0.58 (\pm 0.01) for males in FSA, and 0.30 (\pm 0.02) for females and 0.37 (\pm 0.02) for males in SSA. The parameter S_{95} (the number of individuals within the area of one home range, Efford et al., 2016) was 5.93 for females and 6.75 for males in FSA, and 2.04 for females and 3.06 for males in SSA.

4 | DISCUSSION

Our study shows that density-mediated effects alone are not sufficient to explain changes in mouse spatial behavior evoked by mast seeding. Past studies have generally concluded that masting reduces space use through increased population density (Auger et al., 2016; Mazurkiewicz & Rajska-Jurgiel, 1998; Stradiotto et al., 2009). Our results partly support this prediction, in that σ , the index of home range size, declined with increasing density and was generally lower in FSA compared to SSA years. However, for the same level of density, home

Model structure					
λ_0	D	σ	#P	Δ AICc	w_i
(a) Females					
Behavioral response	Session	Session	230	0	0.86
Session + Behavioral response	Session	(.)	230	3.60	0.14
Session + Behavioral response	Session	Session	329	57.71	<0.001
Behavioral response	Session	(.)	131	100.32	<0.001
Session	Session	(.)	222	111.84	<0.001
(b) Males					
Behavioral response	Session	Session	242	0	1
Session + Behavioral response	Session	Session	347	77.12	<0.001
Session + Behavioral response	Session	(.)	242	107.72	<0.001
Behavioral response	Session	(.)	137	156.52	<0.001
(.)	Session	Session	234	159.57	<0.001

TABLE 1 Model selection table, identifying the most parsimonious models of density and home range of a) females and b) males of yellow-necked mice

Only the best five candidate models are shown.

λ_0 , detection probability; D, density; σ , spatial scale of detection (i.e., metric of home range size); (.), constant; session, varying among trapping sessions. The models were ranked according to Δ AICc; #P denotes the number of parameters, and w_i can be interpreted as the weight of evidence in favor of model i (Burnham & Anderson, 2002).

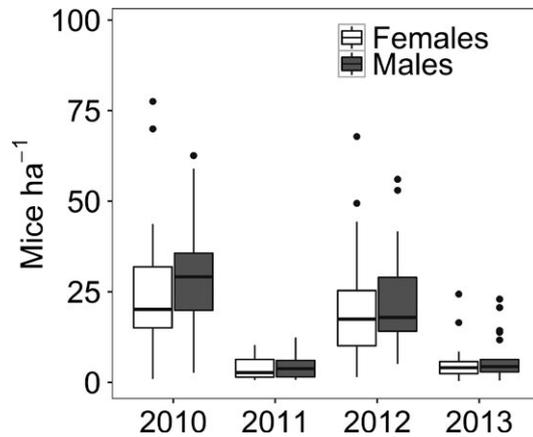


FIGURE 2 Density of females and males of the yellow-necked mouse in Gorzowska Forest (W Poland). Monthly (4 months) site-specific (eight grids) densities are averaged to show differences among years. Beech masting occurred in 2009 and 2011. Density is derived from SECR models that received best AIC support (see Table 1 and Methods for details). Boxes denote 25th, 50th, and 75th percentiles; whiskers represent the lowest and highest datum within the 1.5 interquartile range

TABLE 2 Statistical significance of GLMM fixed effects testing the relationship between mast seeding and rodent space use

Fixed effect	χ^2	<i>p</i>
Mast	28.09	<.001
Sex	3.98	.05
Density	148.71	<.001
Mast × sex	4.40	.03
Mast × density	2.69	.07
Sex × density	0.53	.46

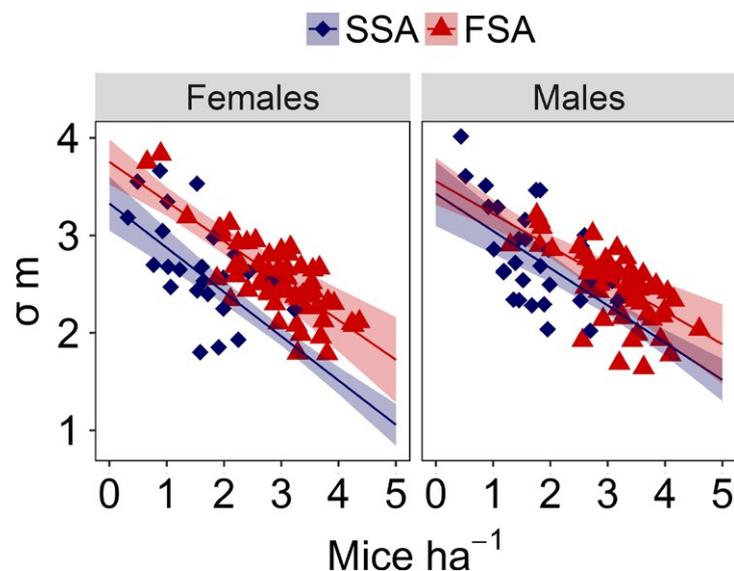
The response variable is log-transformed sigma (i.e., SECR-derived metric of home range size). Study site was used as random effect. Degrees of freedom for all effects equal 1

range sizes were larger in the peak phase of the cycle (FSA) in comparison with the crash phase (SSA). This indicates a higher degree of space overlap between neighboring individuals, as shown by *k* and S_{95} estimates (Efford et al., 2016). It is not clear whether mice are more tolerant of overlap in space use in post-mast years or whether they are constrained to use more space, relative to overall densities. However, it is clear that the effects of mast seeding on space use in mice are more complicated than simple density-mediated changes in space use.

In order to explain the difference in spatial overlap during different phases of the mast-induced population cycle, we need to invoke a mechanism that involves something other than the density itself. Relatedness among individuals would be likely to differ between FSA and SSA summers after masting because, for a given density, post-mast populations are in the peak phase after growth during the mast event, whereas SSA populations have grown to this density after a low density period. When mouse population density rises and territories are filled, dispersal rates typically decline in rodents (Ims & Andreassen, 2000, 2005; Lambin & Krebs, 1991; Smith & Batzli, 2006; Wolff, 1997). This process leads to higher relatedness of neighboring individuals (Andreassen et al., 2013; Pilot et al., 2010; Sutherland, Spencer, Singleton, & Taylor, 2005; Wolff, 1997). Home range overlap is higher between more closely related individuals (Ims, 1989; Kawata, 1990; Lambin & Krebs, 1993; Le Galliard et al., 2006; Wolff, 1997), probably due to reduced aggression (Kawata, 1990; Lambin & Krebs, 1993). This effect occurs in both sexes, but is stronger in females than in males (Innes et al., 2012; Ishibashi, Saitoh, Abe, & Yoshida, 1997; Le Galliard et al., 2006; Pilot et al., 2010), which is consistent with the stronger effect of masting years on female mice in our study.

The pattern of high spatial overlap among individuals in the peak phase of the population cycle found in our study is similar to that found in rodent population cycles that are not driven by masting, but by a set of intrinsic (e.g., sociality, dispersal) and extrinsic

FIGURE 3 Relationship between density of the yellow-necked mouse and sigma (σ , model-derived estimate of home range size) in first summer after masting and second summer after masting years. Dots represent session-specific estimates of parameters. Note that both axes are on log scale. The log-log slope of fitted curves equals -0.5 , while the difference in intercepts indicates differences in home range overlap (i.e., higher intercept denotes larger home ranges for the same level of density). Trend lines are reported with 95% confidence intervals and are based on predictions from generalized linear mixed model (see Methods section for details)



(e.g., predation) factors (Andreassen et al., 2013; Radchuk, Ims, & Andreassen, 2016). In such systems, spatial overlap enhances reproduction at the beginning of the population growth phase, but after a critical point, it triggers population collapse (reviewed in Andreassen et al., 2013). Reproduction is first enhanced because the benefits of sharing space (e.g., protection against infanticide) outpace the costs (e.g., competition for food). In the latter phase, intensified crowding slows down reproduction, and the crash is caused by predation of dominant males, which disrupts social groups and further decreases survival (Andreassen & Gundersen, 2006; Ims & Andreassen, 2000; Odden, Ims, Støen, Swenson, & Andreassen, 2014). Similar sets of intrinsic factors might be responsible for population regulation across a variety of territorial mammals (Odden et al., 2014).

Such processes have not been studied in mast-induced population cycles, although we know that dispersal rates decline during post-mast (peak) years in yellow-necked mouse (Mazurkiewicz & Rajska-Jurgiel, 1998) and that reproduction ceases in the peak phase of the cycle (Falls, Falls, & Fryxell, 2007; Fitzgerald, Efford, & Karl, 2004; Mazurkiewicz & Rajska-Jurgiel, 1998; Pucek et al., 1993; Wolff, 1996). In mast-generated population cycles, rodent abundance is still growing during early summer after masting, although beech seeds are already depleted (consumed, germinated, or rotten), and the decline begins in late summer or autumn (Falls et al., 2007; Pucek et al., 1993; Zwolak et al., 2016). Our study points that the number of individuals within one home range is 2- to 3-fold higher in FSA than in SSA. This is very likely to affect the competition for resources and disease transmission and, thus, play a role in the population decline. In that context, it might be illuminating to study how dispersal, spatial organization, reproduction, and survival covary across the whole mast-induced population cycle.

The increase in spatial overlap of home ranges that was found after mast years could be caused by other factors. Although availability of beech seeds was most likely constant across years (because trapping was conducted when this food source was unavailable), availability of other food items could vary. For example, in conifer forests of North America, masting-mediated increase in density, survival, and reproduction in deer mice (*Peromyscus maniculatus*) was delayed to summer after masting (Lobo & Millar, 2013). Authors suggested that the fir (*Abies lasiocarpa*) masting resulted in population response of invertebrate seed predators that translated into higher prey availability for rodents (Lobo & Millar, 2013). Such an effect could potentially prolong the window of increased food availability after masting into next year summer and affect spatial behavior of mice. Investigating whether masting results in the second-order pulse in invertebrate numbers could be an interesting avenue for future research.

Spatially explicit capture–recapture models provide an effective tool to separate the effects of density on space use from other factors (Efford et al., 2016) and allowed us to show that the patterns of space use differ between distinct phases of rodent population cycle. One advantage is that our research was based on an extensive dataset that allowed the estimation of population-wide changes in space use. This scale is usually infeasible in telemetry-based studies that are necessarily limited to a smaller subsample of individuals. Moreover, live

trapping (or analogous methods based on proximity detectors: Efford, Dawson, & Borchers, 2009b; Efford, 2011) is a widely used research method. This wide use means that SECR models can be applied to separate the effects of density from other important biological factors in a wide range of ecological problems, for example, in studies testing the influence of habitat type on space use, in studies on multi-annual population cycles of voles and lemmings where spacing behavior is likely to be a key component of population regulation (Andreassen et al., 2013; Efford et al., 2016; Wolff, 1997), or to study spacing behavior of pests to inform management policy (Ringler et al., 2014). We hope that our study will encourage future applications of this method.

ACKNOWLEDGMENTS

We thank Leone M. Brown for suggesting SECR models and Murray Efford for his invaluable tips at SECR forum. We thank Nadleśnictwo Bogdaniec for permission to conduct this study at Leśnictwo Wysoka. Sylwia Dziemian-Zwolak, Aleksandra Wróbel, Milena Zduniak, and numerous other AMU students helped during the field work. This study was supported by Polish Ministry of Science and Higher Education Grant No. NN304391537 and Polish National Science Centre Grant No. 2012/04/M/NZ8/00674 awarded to RZ. MB was supported by National Science Centre grant “Etiuda” no. 2015/16/T/NZ8/00018 and by Foundation for Polish Science scholarship “Start.” Participation by EEC and LR was supported through the Wendy and Neil Sandler International Research Program at Tufts University. SECR models were run with support from PLGrid Infrastructure. This research was conducted under the approval of the Local Ethical Commission for Experiments with Animals in Poznań (permits no. 62/2008 and no. 13/2012) and the General Director for Environmental Protection (permit no. DOPozgiz-4200/IV- 43/2800/10/JRO).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Adams, E. S. (2001). Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, 32, 277–303.
- Andreassen, H. P., Glorvigen, P., Rémy, A., & Ims, R. A. (2013). New views on how population- intrinsic and community-extrinsic processes interact during the vole population cycles. *Oikos*, 122, 507–515. doi: 10.1111/j.1600-0706.2012.00238.x
- Andreassen, H. P., & Gundersen, G. (2006). Male turnover reduces population growth: An enclosure experiment on voles. *Ecology*, 87, 88–94. doi: 10.1890/04-1574
- Auger, J., Meyer, S. E., & Jenkins, S. H. (2016). A mast-seeding desert shrub regulates population dynamics and behavior of its heteromyid dispersers. *Ecology and Evolution*, 6, 2275–2296. doi: 10.1002/ece3.2035
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *The Journal of Statistical Software*, 67, 1–48. doi: 10.18637/jss.v067.i01
- Bogdziewicz, M., Zwolak, R., & Crone, E. E. (2016). How do vertebrates respond to mast seeding? *Oikos*, 125, 300–307. doi: 10.1111/oik.03012

- Borchers, D. L., & Efford, M. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, *64*, 377–385.
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology*, *68*, 203–220.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag New York: Springer Science and Business Media.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*, 346–352.
- Crone, E. E., & Rapp, J. (2014). Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, *1322*, 21–34. doi: 10.1111/nyas.12465
- Desy, E., Batzli, G., & Liu, J. (1990). Effects of food and predation on behaviour of prairie voles: A field experiment. *Oikos*, *58*, 159–168. doi: 10.2307/3545423
- Drózd, A. (1966). Food habits and food supply of rodents in the beech forest. *Acta Theriologica*, *16*, 363–384.
- Efford, M. G. (2004). Density estimation in live-trapping studies. *Oikos*, *106*, 598–610. doi: 10.1111/j.0030-1299.2004.13043.x
- Efford, M. G. (2011). Estimation of population density by spatially explicit capture–recapture analysis of data from area searches. *Ecology*, *92*, 2202–2207. doi: 10.1890/11-0332.1
- Efford, M. G. (2015). *secr: Spatially explicit capture-recapture models*. R package version 2.9.4. <http://CRAN.R-project.org/package=secr>
- Efford, M. G., Borchers, D. L., & Byrom, A. E. (2009a). Density estimation by spatially explicit capture–recapture: Likelihood-based methods. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.), *Modeling demographic processes in marked populations: Environmental and ecological statistics* (pp. 255–269). New York, NY: Springer.
- Efford, M. G., Dawson, D. K., & Borchers, D. L. (2009b). Population density estimated from locations of individuals on a passive detector array. *Ecology*, *90*, 2676–2682. doi: 10.1890/08-1735.1
- Efford, M. G., Dawson, D., Jhala, Y., & Qureshi, Q. (2016). Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography*, *39*, 676–688. doi: 10.1111/ecog.01511
- Efford, M. G., & Fewster, R. M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos*, *122*, 918–928. doi: 10.1111/j.1600-0706.2012.20440.x
- Falls, J. B., Falls, E. A., & Fryxell, J. M. (2007). Fluctuations of deer mice in Ontario in relation to seed crops. *Ecological Monographs*, *77*, 19–32. doi: 10.1890/05-1485
- Fitzgerald, B., Efford, M., & Karl, B. (2004). Breeding of house mice and the mast seeding of southern beeches in the Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology*, *31*, 167–184.
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*, 2nd ed. Thousand Oaks, CA: Sage.
- Godsall, B., Coulson, T., & Malo, A. F. (2014). From physiology to space use: Energy reserves and androgenization explain home-range size variation in a woodland rodent. *Journal of Animal Ecology*, *83*, 126–135. doi: 10.1111/1365-2656.12116
- Hilton, G., & Packham, J. (1997). A sixteen-year record of regional and temporal variation in the fruiting of beech (*Fagus sylvatica* L.) in England (1980–1995). *Forestry*, *70*, 7–16. doi: 10.1093/forestry/70.1.7
- Ims, R. A. (1989). Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. *Ecology*, *70*, 607–616.
- Ims, R. A., & Andreassen, H. P. (2000). Spatial synchronization of vole population dynamics by predatory birds. *Nature*, *6809*, 194–196.
- Ims, R. A., & Andreassen, H. P. (2005). Density-dependent dispersal and spatial population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 913–918. doi: 10.1098/rspb.2004.3025
- Innes, R. J., Mceachern, M. B., Van Vuren, D. H., Eadie, J. M., Kelt, D. A., & Johnson, M. L. (2012). Genetic relatedness and spatial associations of dusky-footed woodrats (*Neotoma fuscipes*). *Journal of Mammalogy*, *93*, 439–446. doi: 10.1644/11-MAMM-A-171.1
- Ishibashi, Y., Saitoh, T., Abe, S., & Yoshida, M. (1997). Sex-related spatial kin structure in a spring population of grey-sided voles *Clethrionomys rufocanus* as revealed by mitochondrial and microsatellite DNA analyses. *Molecular Ecology*, *6*, 63–71. doi: 10.1046/j.1365-294X.1997.00152.x
- Jensen, T. S. (1982). Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia*, *54*, 184–192.
- Kawata, M. (1990). Fluctuating populations and kin interaction in mammals. *Trends in Ecology & Evolution*, *5*, 17–20. doi: 10.1016/0169-5347(90)90007-Z
- Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, *12*, 465–470. doi: 10.1016/0169-5347(94)90310-7
- Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Koike, S., Abe, S., ... Kaji, K. (2011). Effect of mast production on home range use of Japanese black bears. *Journal of Wildlife Management*, *75*, 867–875. doi: 10.1002/jwmg.122
- Lacher, T. E., & Mares, M. A. (1996). Availability of resources and use of space in eastern chipmunks, *Tamias striatus*. *Journal of Mammalogy*, *77*, 833–849. doi: 10.2307/1382689
- Lambin, X., & Krebs, C. J. (1991). Can changes in female relatedness influence microtine population dynamics? *Oikos*, *61*, 126–132. doi: 10.2307/3545414
- Lambin, X., & Krebs, C. J. (1993). Influence of female relatedness on the demography of Townsend's vole populations in spring. *Journal of Animal Ecology*, *62*, 536–550. doi: 10.2307/5203
- Lambin, X., & Yoccoz, N. G. (1998). The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. *Journal of Animal Ecology*, *67*, 1–16. doi: 10.1046/j.1365-2656.1998.00181.x
- Le Galliard, J.-F., Gundersen, G., Andreassen, H., & Stenseth, N. (2006). Natal dispersal, interactions among siblings and intrasexual competition. *Behavioral Ecology*, *17*, 733–740. doi: 10.1093/beheco/arl002
- Lobo, N., & Millar, J. S. (2013). Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. *Journal of Animal Ecology*, *82*, 814–825.
- Mazurkiewicz, M., & Rajska-Jurgiel, E. (1998). Spatial behaviour and population dynamics of woodland rodents. *Acta Theriologica*, *43*, 137–162. doi: 10.1111/1365-2656.12062
- McLoughlin, P. D., & Ferguson, S. H. (2000). A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*, *7*, 123–130.
- McShea, W. J., & Schwede, G. (1993). Variable acorn crops: Responses of white-tailed deer and other mast consumers. *Journal of Mammalogy*, *74*, 999–1006. doi: 10.2307/1382439
- Odden, M., Ims, R. A., Støen, O. G., Swenson, J. E., & Andreassen, H. P. (2014). Bears are simply voles writ large: Social structure determines the mechanisms of intrinsic population regulation in mammals. *Oecologia*, *175*, 1–10. doi: 10.1007/s00442-014-2892-z
- Ostfeld, R. S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology & Evolution*, *5*, 411–415. doi: 10.1016/0169-5347(90)90026-A
- Ostfeld, R. S., & Keasing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, *15*, 232–237. doi: 10.1016/S0169-5347(00)01862-0
- Pedersen, A. B., & Greives, T. J. (2008). The interaction of parasites and resources cause crashes in a wild mouse population. *Journal of Animal Ecology*, *77*, 370–377. doi: 10.1111/j.1365-2656.2007.01321.x
- Pilot, M., Dąbrowski, M. J., Jancewicz, E., Schtickzelle, N., & Gliwicz, J. (2010). Temporally stable genetic variability and dynamic kinship structure in a fluctuating population of the root vole *Microtus oeconomus*. *Molecular Ecology*, *19*, 2800–2812. doi: 10.1111/j.1365-294X.2010.04692.x
- Proffitt, K. M., White, P. J., & Garrott, R. A. (2010). Spatio-temporal overlap between Yellowstone bison and elk—implications of wolf restoration and other factors for brucellosis transmission risk. *Journal of Applied Ecology*, *47*(2), 81–289. doi: 10.1111/j.1365-2664.2010.01770.x
- Pucek, Z., Jedrzejewski, W., Jedrzejewska, B., & Pucek, M. (1993). Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica*, *38*, 199–199.

- Radchuk, V., Ims, R. A., & Andreassen, H. P. (2016). From individuals to population cycles: The role of extrinsic and intrinsic factors in rodent populations. *Ecology*, *97*, 720–732. doi: 10.1890/15-0756.1
- Ringler, D., Russel, J., Jaeger, A., Pinet, P., Bastien, M., & Le Corre, M. (2014). Invasive rat space use on tropical islands: Implications for bait broadcast. *Basic and Applied Ecology*, *15*, 176–186. doi: 10.1016/j.baae.2014.01.005
- Schmidt, K. A., & Ostfeld, R. S. (2003). Mice in space: Space use predicts the interaction between mice and songbirds. *Ecology*, *84*, 3276–3283. doi: 10.1890/02-0643
- Schoepf, I., Schmohl, G., König, B., Pillay, N., & Schradin, C. (2015). Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Animal Behaviour*, *99*, 53–60. doi: 10.1016/j.anbehav.2014.10.002
- Selva, N., Hobson, K. A., Cortés-Avizanda, A., Zalewski, A., & Donazar, J. A. (2012). Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. *PLoS ONE*, *7*(12), e51267. doi: 10.1371/journal.pone.0051267
- Smith, E. J., & Batzli, O. G. (2006). Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: A field experiment. *Oikos*, *112*, 209–217. doi: 10.1111/j.0030-1299.2006.13431.x
- Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., & Rizzoli, A. (2009). Spatial organization of the yellow-necked mouse: Effects of density and resource availability. *Journal of Mammalogy*, *90*, 704–714. doi: 10.1644/08-MAMM-A-120R1.1
- Sutherland, D. R., Spencer, P., Singleton, G. R., & Taylor, A. C. (2005). Kin interactions and changing social structure during a population outbreak of feral house mice. *Molecular Ecology*, *14*, 2803–2814. doi: 10.1111/j.1365-294X.2005.02623.x
- Wolff, J. O. (1996). Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy*, *77*(3), 850–856.
- Zwolak, R., Bogdziewicz, M., & Rychlik, L. (2016). Beech mast-ing modifies the response of rodents to forest management. *Forest Ecology and Management*, *359*, 268–276. doi: 10.1016/j.foreco.2015.10.017

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Bogdziewicz, M., Zwolak, R., Redosh, L., Rychlik, L. and Crone, E. E. (2016), Negative effects of density on space use of small mammals differ with the phase of the mast-ing-induced population cycle. *Ecology and Evolution*, *00*: 1–8. doi: 10.1002/ece3.2513



Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe

Michał Bogdziewicz^{a,*}, Jakub Szymkowiak^b

^aDepartment of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61–614 Poznań, Poland

^bDepartment of Avian Biology and Ecology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61–614 Poznań, Poland

Received 16 June 2015; accepted 7 January 2016
Available online 15 January 2016

Abstract

Lyme disease is a major zoonosis in the northern hemisphere. It is caused by the spirochete *Borrelia burgdorferi*, transmitted by ticks (genus *Ixodes*), and the abundance of infected tick nymphs determines the risk of the disease in humans. In eastern USA, fluctuations in oak (*Quercus* spp.) acorn production (including mast seeding) determine rodent abundance, which has been linked with Lyme borreliosis risk in humans. However, the predictive power of masting on Lyme disease risk in other systems has never been tested. We used a combination of field and Internet data to trace the ecological chain reaction that links acorn production by oaks and Lyme borreliosis risk in European forests. We found a positive relationship between oak acorn production (*Q. robur* and *Q. petraea*) in year T and the number of Lyme borreliosis incidences in year $T+2$. Acorn production was also positively correlated with Google search volume for the terms “tick” and “Lyme disease” two years later. Our results suggest that acorn production influences tick population, leading to fluctuations in the intensity of interactions between humans and ticks that can be seen in Google search dynamics. Thus, mast seeding together with the volume of specific Internet web searches appears to be a promising tool that could be used to alert public.

Zusammenfassung

Die Lyme-Borreliose ist eine bedeutende Zoonose der nördlichen Hemisphäre. Sie wird von dem Spirochäten *Borrelia burgdorferi* verursacht und von Zecken (Gattung *Ixodes*) übertragen. Mit der Abundanz infizierter Zeckennymphen steigt das Krankheitsrisiko für den Menschen. In den östlichen USA bestimmen die Schwankungen der Eichelproduktion (*Quercus* spp.) mit dem Auftreten von Mastjahren die Abundanz der Kleinsäuger, die mit dem Lyme-Borreliose-Risiko für den Menschen in Zusammenhang gebracht wurde. In anderen Gegenden wurde die Vorhersagekraft der Mastjahre noch nicht getestet. Wir nutzten eine Kombination aus Freiland- und Internetdaten, um die ökologische Wirkungskette aufzuspüren, die Eichelproduktion und das Lyme-Borreliose-Risiko in europäischen Wäldern verbindet. Wir fanden eine positive Korrelation zwischen Eichelproduktion (*Q. robur* and *Q. petraea*) im Jahr T und der Anzahl von Lyme-Borreliose-Fällen im Jahr $T+2$. Die Eichelproduktion war

*Corresponding author. Tel.: +48 061 829 5800; fax: +48 61 829 56 36.

E-mail addresses: michalbogdziewicz@gmail.com, micbog@amu.edu.pl (M. Bogdziewicz).

auch positiv mit dem Google-Suchvolumen für “Zecke” und “Lyme-Borreliose” im Jahr $T+2$ korreliert. Unsere Ergebnisse legen nahe, dass die Eichelproduktion die Zeckenpopulation beeinflusst, was zu Schwankungen der Intensität der Interaktionen zwischen Mensch und Zecke führt, wie wir sie bei der Google-Suche beobachten können. Damit scheinen Eichelmast und Internet-Recherchen ein vielversprechendes Mittel zu sein, das für Warnungen an die Bevölkerung genutzt werden kann.

© 2016 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Google Trends; *Ixodes scapularis*; *Ixodes ricinus*; Mast seeding; Rodent outbreak; Zoonotic disease

Introduction

Lyme borreliosis is the most common zoonosis and a major health concern in the northern hemisphere (Barbour & Fish 1993; Pfäffle, Littwin, Muders, & Petney 2013). It is caused by *Borrelia burgdorferi* sensu lato transmitted by hard-bodied ticks (genus *Ixodes*), and the abundance of infected tick nymphs is a good predictor of the disease risk in humans (Barbour & Fish 1993; Ostfeld 2010; Stafford, Cartter, Magnarelli, Ertel, & Mshar 1998). In the eastern United States temporal fluctuations in oak (*Quercus* spp.) acorn production (mast seeding: Crone & Rapp 2014; Kelly 1994) cause temporal variation in food provision for granivorous rodents, which shapes their population dynamics (McShea 2000; Wolff 1996). This in turn influences the abundance of infected tick nymphs and the risk of Lyme disease in humans (Jones, Ostfeld, Richard, Schaubert & Wolff 1998a; Ostfeld 2010; Ostfeld, Canham, Oggenfuss, Winchcombe, & Keesing 2006; Ostfeld, Jones, & Wolff 1996; Schaubert, Ostfeld, & Evans 2005). However, the connection between mast seeding and Lyme disease in the eastern United States has been disputed, given the variety of factors that may contribute to the disease risk (Estrada-Pena 2009; Randolph 1998).

The ecological link between mast seeding and Lyme disease in eastern United States is as follows. In summer after a good acorn year, host-seeking larvae of the blacklegged tick (*Ixodes scapularis*) co-occur with high abundance of rodents caused by previous year surplus food supply (Jones et al. 1998a; Ostfeld et al. 2006; Ostfeld et al. 2001). High rodent numbers increase larval feeding chances and survival, which leads to high nymph densities next season (Keesing et al. 2009; Ostfeld 2010; Ostfeld et al. 2006). Moreover, high reservoir-competence of rodent hosts increases *B. burgdorferi* prevalence among tick nymphs (Ostfeld et al. 2001, 2006). Next spring, numerous infected nymphs search for vertebrate hosts, including humans (Schauber et al. 2005). Nymphs are mostly responsible for transmitting Lyme disease to humans because their small size makes them difficult to detect. Moreover, their summer peak in activity coincides with the peak of human outdoor activity (Barbour & Fish 1993; Ostfeld 2010). Thus, oak acorn production in year T influences rodent abundance next year ($T+1$), which subsequently affects infected nymph abundance and Lyme disease risk in year $T+2$ (Barbour & Fish 1993; Ostfeld et al. 2001, 2006; Schaubert et al. 2005).

Fluctuations in oak acorn production have similar effects on wildlife in Europe (Bogdziewicz, Zwolak, & Crone 2016; Jędrzejewska, & Jędrzejewski 1998; Pucek, Jędrzejewski, Jędrzejewska, & Pucek 1993), but the effects of oak mast seeding on the incidence of Lyme disease have not been studied. Seed fall in autumn determines rodent abundance next summer (Jensen 1982; Pucek et al. 1993; Zwolak, Bogdziewicz, & Rychlik 2016), and small mammals are a good reservoir for the *Borrelia* spirochete (Franke, Hildebrandt, & Dorn 2013; Gern 2008; Michalik, Hofman, Buczek, Skoracki, & Sikora 2003; Siński, Pawelczyk, Bajer, & Behnke 2006). Moreover, the sheep tick (*Ixodes ricinus*), ecological equivalent of *I. scapularis* in the European host–tick–pathogen system, has similar ecology to the blacklegged tick (Barbour & Fish 1993; Beytout et al. 2007; Hubálek, Halouzka, & Juřicová 2003; Korenberg, Kovalevskii, & Gorelova 2002; Siński et al. 2006). Thus, we hypothesize that a similar chain of ecological events linking acorn production and Lyme borreliosis risk might occur in Europe.

Traditional methods of gathering ecological data can be supplemented with new technologies. Temporal fluctuations in Google search volume and Wikipedia logs have been used to forecast influenza, dengue or tuberculosis outbreaks (Generous, Fairchild, Deshpande, Del Valle, & Friedhorsky 2014; Ginsberg et al. 2008; McIver & Brownstein 2014). In a recent study, Google Trends were successfully used to collect national-scale data on fluctuations in rodent numbers, to study the role of rodent predation pressure in wood warbler (*Phylloscopus sibilatrix*) habitat selection (Szymkowiak & Kuczyński 2015). Indices of rodent abundance obtained using Google search engine were positively validated with field data (see details in Szymkowiak & Kuczyński 2015). Here, we used temporal changes in Google search volume to trace ecological chain reactions linking acorn production with Lyme disease risk. We assumed that people use the Internet as a source of information about ticks and Lyme disease. Hence, an increase in number of interactions between humans and ticks should lead to increase in the search volume of focal keywords. We selected two unambiguous keywords i.e., “kleszcz” (which stands for tick in Polish) and “borelioza” (Lyme disease), and calculated search volumes for each year of the study period. Moreover, we calculated search volumes for the term “na myszy” (in Polish: something for/against mice, hereafter “mice”) for each year as this appears to

provide a reliable index of annual fluctuations in rodent numbers (cf. Szymkowiak & Kuczyński 2015).

We used our dataset to test the predictions derived from Ostfeld et al.'s works (referenced above). First, acorn production should positively influence rodent numbers (e.g. Pucek et al. 1993). Thus, we tested whether acorn production in year T positively correlates with Google index of mice abundance in year $T + 1$. Second, the positive effect of acorn production (year T) on rodent numbers (year $T + 1$) should translate into increase in intensity of tick-human interactions and, consequently, Lyme disease cases (in year $T + 2$). Thus, we tested whether Google index of rodent abundance in year $T + 1$ correlates positively with Google search volume for “tick” in year $T + 2$. Next, we tested whether acorn production (year T) correlates positively with Lyme disease-related key words (“tick” and “Lyme disease”), and Lyme disease cases in year $T + 2$. To our knowledge, this is the first study linking temporal fluctuations in acorn production with Lyme disease risk in Europe. Our research answers the call of Jones et al. (1998b), “Nevertheless, we hope that epidemiologists will test the power of acorn production as a predictor of Lyme disease risk in European oak forests”, which stayed ignored for almost 20 years.

Materials and methods

Data collection

We extracted the epidemiological data on the number of reported cases of Lyme disease in Poland from annual (2006–2013) reports on infectious diseases (Fig. 1B). These data were collected by the Provincial Sanitary–Epidemiological Stations and provided by the National Institute of Public Health–National Institute of Hygiene in Poland (<http://www.pzh.gov.pl/>).

Data on annual acorn production of pedunculate (*Quercus robur*) and sessile oak (*Q. petraea*) were collected in years 2005–2011 for the purpose of the Polish Forest Gene Bank, and provided by the State Forests in Poland. Each year, oak seed crop was assessed in September and October on permanent forest plots which were evenly distributed across all 17 Regional Directorates of the State Forests (RDSF) in Poland. The median area surveyed in each year was 25,988.77 ha ($Q_{25}–Q_{75}\% = 25,441.09–26,059.23$). Acorns were collected from the forest floor and by using standard seed traps. Considering that the area surveyed during the study period was unequal among years, we calculated the mean amount of acorns (kg/ha) collected in each year by all RDSFs and used it as a measure of annual acorn production across the country (Fig. 1A). We used oak masting as a predictor of Lyme disease risk because the geographical range of these two species (*Q. robur* and *Q. petraea*) covers the whole country (which corresponds to the spatial scale of other variables, see below), it dominates deciduous stands across the

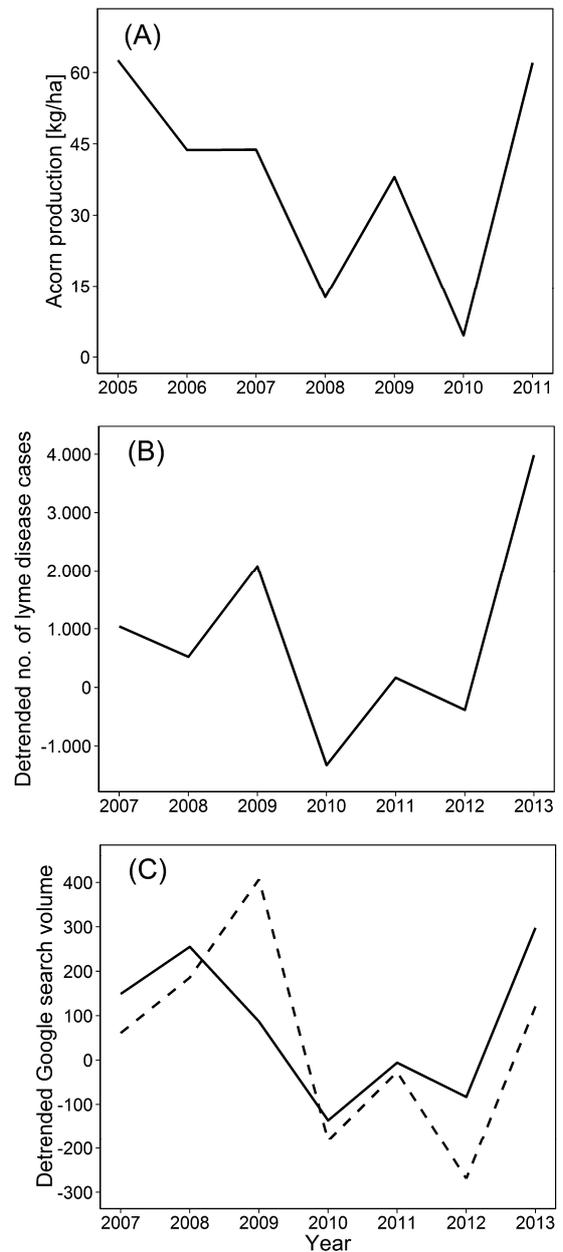


Fig. 1. Time series showing (A) acorn production, (B) detrended number of reported Lyme disease cases, and (C) detrended Google search volume for term “tick” (solid line), and “Lyme disease” (dashed line), in Poland.

country, and oak acorn production is highly synchronized across Poland (Kantorowicz 2000).

We used the search query series from the Google Trends website to calculate the yearly (2006 to 2013) search volumes of specific Lyme – and tick – related keywords in Google search engine, and tracked how these volumes changed over time (Fig. 1C). We used 2006 as the first data point because it was the first year when Google search engine market share exceeded the share of all other web search engines in Poland (Megapanel PBI/Gemius). Google

Table 1. Models testing predictions on acorn production – Lyme disease risk association derived from Ostfeld et al.'s works (referenced in the main text). “Google” indicates Google search volume obtained from Google Trends (see the Materials and methods section for details). Data was detrended before analysis. Each row represents a separate model.

Predictor	Response	Model estimate	SE	<i>t</i> Value	<i>p</i> Value	<i>R</i> ²
Acorn production in year <i>T</i>	Google for “mice” in year <i>T</i> +1	9.49	7.493	1.27	0.274	0.11
	Google for “tick” in year <i>T</i> +2	6.28	1.727	3.64	0.015	0.67
	Lyme disease cases in year <i>T</i> +2	60.4	21.94	2.75	0.04	0.52
	Google for “Lyme disease” in year <i>T</i> +2	7.1	3.26	2.18	0.082	0.38
Google for “mice” in year <i>T</i>	Google for “tick” in year <i>T</i> +1	0.34	0.138	2.48	0.056	0.46
Google for “tick” in year <i>T</i>	Lyme disease cases in year <i>T</i>	8.43	2.843	2.96	0.031	0.56
Google for “Lyme disease” in <i>T</i>	Lyme disease cases in year <i>T</i>	5.03	2.571	1.96	0.108	0.32

keywords (“tick”, “mice”, “Lyme disease”) were chosen *a priori*, before we started working with the internet data. Because Google Trends data are reported by country and language, the spatial scale of collected internet metrics corresponds to spatial scale of acorn production data and Lyme disease cases (all national).

Internet popularity and awareness for tick-borne diseases are increasing, leading to an overall increasing trend of Google search volume and reported numbers of Lyme disease cases over recent years. Thus, we detrended these variables using the first-order differencing method (Box, Jenkins, & Reinsel 2013; Cowpertwait & Metcalfe 2009), which allowed

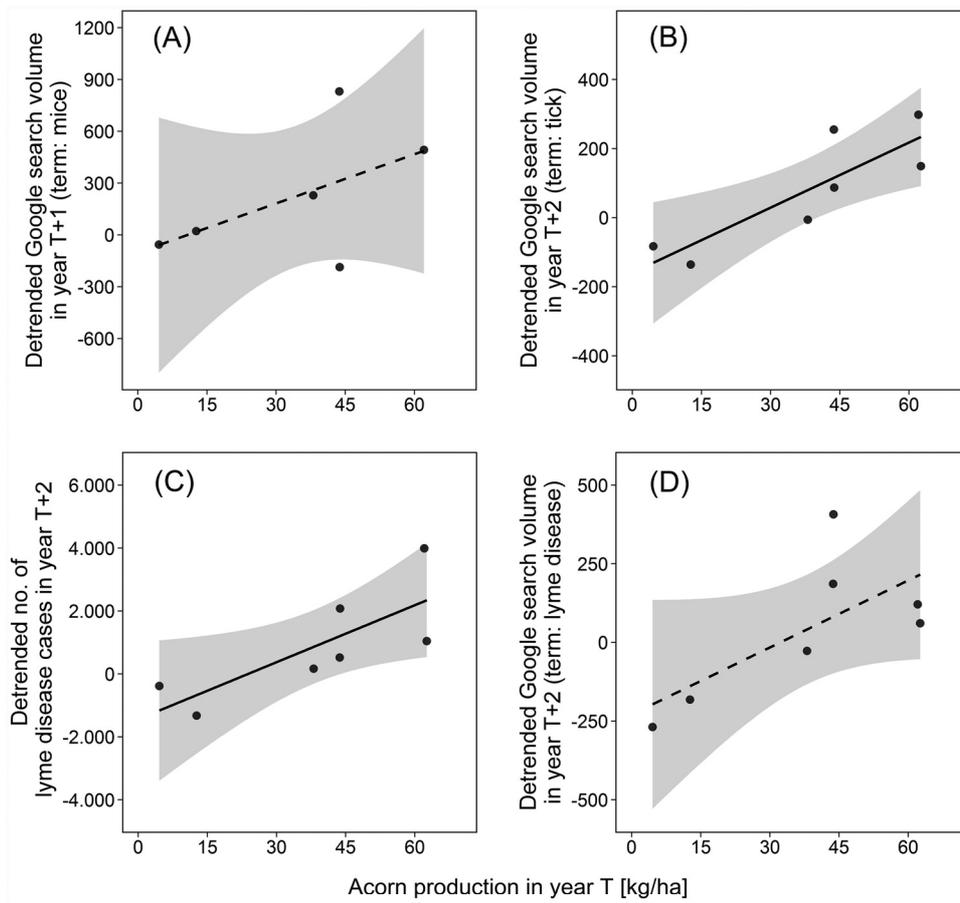


Fig. 2. Generalized linear models representing the modeled effect of oaks acorn production in year *T* on (A) Google search volume for the term “mice” in year *T*+1, (b) Google search volume for the term “tick” in year *T*+1, (C) number of Lyme disease cases in year *T*+2, and (D) Google search volume for the term “Lyme disease” in year *T*+2. Shaded regions represent 95% confidence intervals, and dots represent data points. Dashed lines represent non-significant relationships. Negative values on axes are the result of data detrending (see the Materials and methods section).

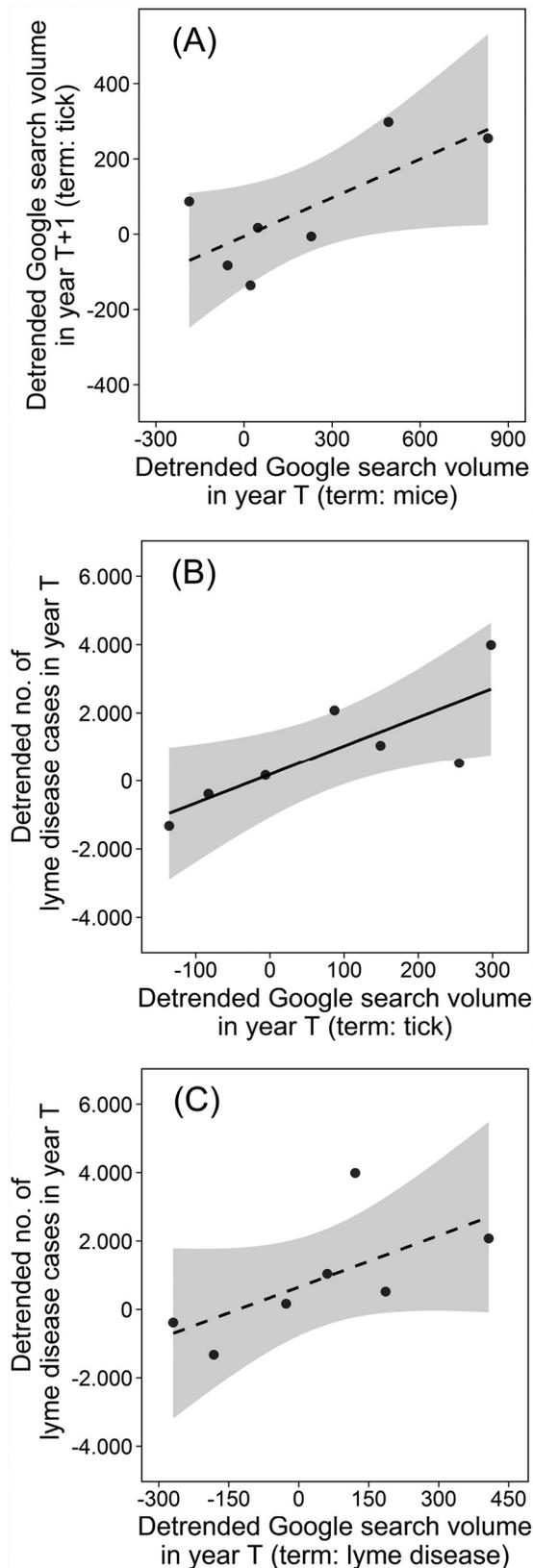


Fig. 3. Generalized linear models representing the modeled effect of (A) Google search volume for the term “mice” in year T on Google search volume for the term “tick” in year $T+1$, and effects of (B) Google search volume for the term “tick” in year T , and (C)

us to analyze their fluctuations not explained by increasing temporal trend itself.

Analysis

We used Generalized Linear Models (GLMs) to test for the relationships between oak acorn production, number of Lyme disease cases, and Google search volume of borreliosis-related keywords (summarized in Table 1). We tested whether acorn production in year T is a good predictor of Google search volume for “mice” (year $T+1$), “tick” (year $T+2$), “Lyme disease” (year $T+2$), and Lyme disease cases (year $T+2$). Next, we tested whether Google search volume for “mice” (year $T+1$) is positively correlated with Google search volume for “tick” (year $T+2$). Moreover, we tested whether the number of reported Lyme disease cases correlates positively with Google search volume of Lyme disease-related key words (“tick” and “Lyme disease”) in the same year.

To provide stronger inference, we fitted the same models but the time lags between response and predictor variables were rearranged (we subtracted one year from all lags). In this set of models the relationships not matched the mechanistic link between acorns, rodents, ticks, and Lyme disease described in the Introduction section; thus, no correlation should be expected. This approach allowed, at least partially, to address the possibility of obtaining spurious correlations between analyzed time-series. We used R version 3.1.2 for performing statistical analysis (R Development Core Team 2013). The normality of residuals was assessed by graphical inspection of residual patterns and Shapiro–Wilk test.

Results

As hypothesized, acorn production in year T was a good predictor of the number of Lyme disease cases in year $T+2$ (Table 1 and Fig. 2C). We also found a positive correlation between acorn production in year T and Google search volume for “tick” in year $T+2$ (Table 1 and Fig. 2B). Moreover, there was a positive correlation between acorn production in year T and Google search volume for “mice” ($T+1$) and “Lyme disease” ($T+2$) (Fig. 2A and D), but both relationships were not significant at $\alpha = 0.05$ level (Table 1).

Google search volume for “mice” (year $T+1$) tended to be positively related with the search volume for “tick” (year $T+2$) (Table 1 and Fig. 3A). Finally, the number of Lyme

Google search volume for the term “Lyme disease” in year T , on the number of Lyme disease cases in year T . Shaded regions represent 95% confidence intervals, and dots represent data points. Dashed lines represent non-significant relationships. Negative values on axes are the result of data detrending (see the Materials and methods section).

disease cases in year T was positively correlated with Google search volumes for Lyme disease-related key-words (“tick” and “Lyme disease”) (Fig. 3B and C), but only the first relationship was significant (Table 1).

None of the relationships with rearranged time lags between response and predictor variables was significant. Acorn production was not correlated with Lyme disease cases, nor with Google search volume for “mice”, and “Lyme disease” in the same year (all $p \geq 0.30$). The relationship between Google search volumes for “mice” and “tick” in year T was negative and not significant ($p = 0.58$). Finally, no relationships were found between Lyme disease cases in year T and Lyme-disease related key words in year $T - 1$ (all $p \geq 0.23$).

Discussion

Risk of acquiring Lyme disease by humans is directly linked with the abundance and distribution of questing ticks. Thus, it is essential to understand factors shaping tick population dynamics. We used a combination of three sources of the data: National Institute of Hygiene in Poland on Lyme disease incidence, Polish State Forests on oak acorn crop, and Google Trends, and demonstrated that oak acorn production is associated with the Lyme disease risk in humans. The increase in Google searches for “tick” two years after a good acorn year most likely reflects the increase in the number of humans bitten by ticks. Increase in this internet search coincided with the number of diagnosed cases of Lyme disease which supports the contention that focal search terms indicate fluctuating disease risk.

Host importance for the total tick infection prevalence depends on the proportion of parasite population fed by the host (Brunner & Ostfeld 2008; Ostfeld 2010). Rodent hosts have a great impact on tick infection prevalence in the eastern US because they are abundant and heavily infested with ticks (Keesing et al. 2009; Ostfeld 2010). Moreover, they are highly competent vectors (Mather, Wilson, Moore, Ribeiro, & Spielman 1989) that are inefficient in killing ticks while grooming (Keesing et al. 2009). Hence, larvae that feed on rodents have a high probability of getting infected and to survive until molting into a nymph (Keesing et al. 2009). All these characteristics also hold for European rodents. They reach extreme densities after mast years (Jensen 1982; Pucek et al. 1993; Zwolak et al. 2016), may harbor numerous tick individuals (Harrison, Scantlebury, & Montgomery 2010; Kiffner, Vor, Hagedorn, Niedrig, & R  he 2011; Perkins, Cattadori, Tagliapietra, Rizzoli, & Hudson 2003), and are a highly competent reservoir of *Borrelia* spirochete (Gern et al. 1998; Hanincova et al. 2003). Moreover, survival of ticks feeding on rodents might be exceptionally high. For example, the percentage of larvae that reaches full engorgement while feeding on wood mouse (*Apodemus sylvaticus*) ranges from 72 to 100% (Randolph 1979). Importantly, the positive effect of rodent numbers on abundance of infected nymphs

in Europe has been already established (Beytout et al. 2007; Paziewska, Zwolińska, Harris, Bajer, & Siński 2010; Siński et al. 2006), such as the impact of infected nymph number on Lyme disease risk (Beytout et al. 2007; Hubálek et al. 2003; Jaenson et al. 2009). Here, we added oak mast seeding to the picture, likely providing a more comprehensive view on ecological phenomena shaping temporal variation in risk of acquiring Lyme disease by humans in Europe.

New data sources resulting from human use of the internet offer new perspectives on cheap and fast data collection. Recently, ecologists start to utilize it to gather data that would otherwise be logistically or economically infeasible to collect. For example, Google Street View was used to remotely extract data on nesting habitat of vultures and saved 49.5% of funds (Olea & Mateo-Tomás 2013). Google score was also used to measure popularity of bird and butterfly species among public to facilitate the choice of flagship species (Żmihorski, Dziarska-Pałac, Sparks, & Tryjanowski 2013), or to assess public interest in wetland conservation (Do, Kim, Lineman, Kim, & Joo 2015). Here, we combined field and internet data to trace the chain of ecological reactions that was documented previously in the USA with extensive field sampling.

Given the complicated ecology of Lyme disease (Randolph 2001; Ostfeld 2010), such a clear signal found in our study provides reliable support for the notion that Lyme disease risk can be predicted using mast seeding data (Jones et al. 1998a; Randolph 1998; Schaubert et al. 2005). Nevertheless, inclusion of longer time series and data from other European countries would be a valuable direction of future research. In western Europe, fluctuations in rodent numbers caused by mast seeding were shown to correlate with other zoonoses, especially with nephropathia epidemica caused by rodent-borne hantaviruses (Clement, Vercauteren, Verstraeten, Ducoffre, Barrios et al. 2009; Tersago et al. 2009). Thus, a good seed year may serve as a first indicator of imminent increase in rodent-borne disease risk. Moreover, effect of masting on Google search volumes (tick, mice) may be further used as cues.

Acorn production cannot be experimentally manipulated at a scale large enough to affect Lyme disease incidence in humans. Thus, causality must be cautiously inferred from correlative studies at large scales (Schauber et al. 2005). Ideally, such studies should be followed up by small scale experiments that test proposed mechanisms (Jones et al. 1998a; Schaubert et al. 2005). Here, we showed the link for temperate forest of Eastern Europe and outlined a promising area of future experimental research.

Acknowledgements

We would like to thank Rafał Zwolak and Anonymous Reviewers for critical comments on previous versions of our manuscript. The work was done while MB was supported by Polish National Science Centre grant

“Harmonia” no. 2012/04/M/NZ8/00674, Adam Mickiewicz Foundation Scholarship awarded in 2014, and NCN “Etiuda” grant no. 2015/16/T/NZ8/00018. JSZ was supported by Polish National Science Centre grant “Preludium” no. 2012/07/N/NZ8/00129. We are grateful to Jerzyna Przypaśniak from the State Forests in Poland for sharing the data about oaks seed crop.

References

- Barbour, A. G., & Fish, D. (1993). The biological and social phenomenon of Lyme disease. *Science*, *260*, 1610–1616.
- Beytout, J., George, J., Malaval, J., Garnier, M., Beytout, M., Baranton, G., et al. (2007). Lyme borreliosis incidence in two French departments: Correlation with infection of *Ixodes ricinus* ticks by *Borrelia burgdorferi* sensu lato. *Vector-Borne and Zoonotic Diseases*, *7*, 507–518.
- Bogdziewicz, M., Zwolak, R., & Crone, E. E. (2016). How do vertebrates respond to mast seeding? *Oikos*, <http://dx.doi.org/10.1111/oik.03012>
- Box, G. E., Jenkins, G. M., & Reinsel, G. C. (2013). *Time series analysis: Forecasting and control*. New Jersey: John Wiley & Sons.
- Brunner, J. L., & Ostfeld, R. S. (2008). Multiple causes of variable tick burdens on small-mammal hosts. *Ecology*, *89*, 2259–2272.
- Clement, J., Vercauteren, J., Verstraeten, W. W., Ducoffre, G., Barrios, J. M., Vandamme, A.-M., et al. (2009). Relating increasing hantavirus incidences to the changing climate: The mast connection. *International Journal of Health Geographics*, *8*, 1.
- Cowpervait, P. S., & Metcalfe, A. V. (2009). *Introductory time series with R*. New York: Springer.
- Crone, E. E., & Rapp, J. M. (2014). Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, *1322*, 21–34.
- Do, Y., Kim, J. Y., Lineman, M., Kim, D. K., & Joo, G. J. (2015). Using internet search behavior to assess public awareness of protected wetlands. *Conservation Biology*, *29*, 271–279.
- Estrada-Pena, A. (2009). Tick-borne pathogens, transmission rates and climate change. *Frontiers in Bioscience*, *14*, 2674–2687.
- Franke, J., Hildebrandt, A., & Dorn, W. (2013). Exploring gaps in our knowledge on Lyme borreliosis spirochaetes—updates on complex heterogeneity, ecology, and pathogenicity. *Ticks and Tick-Borne Diseases*, *4*, 11–25.
- Generous, N., Fairchild, G., Deshpande, A., Del Valle, S. Y., & Priedhorsky, R. (2014). Global disease monitoring and forecasting with wikipedia. *PLoS Computational Biology*, *10*, e1003892.
- Gern, L. (2008). *Borrelia burgdorferi* sensu lato, the agent of lyme borreliosis: Life in the wilds. *Parasite*, *15*, 244–247.
- Gern, L., Estrada-Pena, A., Frandsen, F., Gray, J., Jaenson, T., Jongejan, F., et al. (1998). European Reservoir Hosts of *Borrelia burgdorferi* sensu lato. *Zentralblatt für Bakteriologie*, *287*, 196–204.
- Ginsberg, J., Mohebbi, M. H., Patel, R. S., Brammer, L., Smolinski, M. S., & Brilliant, L. (2008). Detecting influenza epidemics using search engine query data. *Nature*, *457*, 1012–1014.
- Hanincova, K., Schäfer, S., Etti, S., Sewell, H.-S., Taragelova, V., Ziak, D., et al. (2003). Association of *Borrelia afzelii* with rodents in Europe. *Parasitology*, *126*, 11–20.
- Harrison, A., Scantlebury, M., & Montgomery, W. (2010). Body mass and sex-biased parasitism in wood mice *Apodemus sylvaticus*. *Oikos*, *119*, 1099–1104.
- Hubálek, Z., Halouzka, J., & Juřicová, Z. (2003). Longitudinal surveillance of the tick *Ixodes ricinus* for borreliae. *Medical and Veterinary Entomology*, *17*, 46–51.
- Jaenson, T. G., Eisen, L., Comstedt, P., Mejlon, H., Lindgren, E., Bergström, S., et al. (2009). Risk indicators for the tick *Ixodes ricinus* and *Borrelia burgdorferi* sensu lato in Sweden. *Medical and Veterinary Entomology*, *23*, 226–237.
- Jędrzejewska, B., & Jędrzejewski, W. (1998). *Predation in vertebrate communities: The Białowieża Primeval Forest as a case study*. Berlin: Springer.
- Jensen, T. S. (1982). Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia*, *54*, 184–192.
- Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M., & Wolff, J. O. (1998a). Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science*, *279*, 1023–1026.
- Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M., & Wolff, J. O. (1998b). Mast seeding and Lyme disease. *Trends in Ecology & Evolution*, *13*, 506.
- Kantorowicz, W. (2000). Half a century of seed years in major tree species of Poland. *Silvae Genetica*, *49*, 245–248.
- Keesing, F., Brunner, J., Duerr, S., Killilea, M., LoGiudice, K., Schmidt, K., et al. (2009). Hosts as ecological traps for the vector of Lyme disease. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3911–3919.
- Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, *9*, 465–470.
- Kiffner, C., Vor, T., Hagedorn, P., Niedrig, M., & Rühle, F. (2011). Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas, Germany. *Parasitology Research*, *108*, 323–335.
- Korenberg, E. I., Kovalevskii, Y. V., & Gorelova, N. B. (2002). Tick–host–*Borrelia* population interactions: Long-term records in Eastern Europe. *Experimental & Applied Acarology*, *28*, 225–229.
- Mather, T. N., Wilson, M. L., Moore, S. I., Ribeiro, J. M., & Spielman, A. (1989). Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). *American Journal of Epidemiology*, *130*, 143–150.
- McIver, D. J., & Brownstein, J. S. (2014). Wikipedia usage estimates prevalence of influenza-like illness in the United States in near real-time. *PLoS Computational Biology*, *10*, e1003581.
- McShea, W. J. (2000). The influence of acorn crops on annual variation in rodent and bird populations. *Ecology*, *81*, 228–238.
- Michalik, J., Hofman, T., Buczek, A., Skoracki, M., & Sikora, B. (2003). *Borrelia burgdorferi* sl in *Ixodes ricinus* (Acari: Ixodidae) ticks collected from vegetation and small rodents in recreational areas of the city of Poznań. *Journal of Medical Entomology*, *40*, 690–697.
- Olea, P. P., & Mateo-Tomás, P. (2013). Assessing species habitat using google street view: A case study of cliff-nesting vultures. *PLoS ONE*, *8*, e54582.
- Ostfeld, R. (2010). *Lyme disease: The ecology of a complex system*. New York: Oxford University Press.
- Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J., & Keesing, F. (2006). Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biology*, *4*, e145.

- Ostfeld, R. S., Jones, C. G., & Wolff, J. O. (1996). Of mice and mast. *BioScience*, *46*, 323–330.
- Ostfeld, R. S., Schaubert, E. M., Canham, C. D., Keesing, F., Jones, C. G., & Wolff, J. O. (2001). Effects of acorn production and mouse abundance on abundance and *Borrelia burgdorferi* infection prevalence of nymphal *Ixodes scapularis* ticks. *Vector Borne and Zoonotic Diseases*, *1*, 55–63.
- Paziewska, A., Zwolińska, L., Harris, P. D., Bajer, A., & Siński, E. (2010). Utilisation of rodent species by larvae and nymphs of hard ticks (Ixodidae) in two habitats in NE Poland. *Experimental and Applied Acarology*, *50*, 79–91.
- Perkins, S. E., Cattadori, I. M., Tagliapietra, V., Rizzoli, A. P., & Hudson, P. J. (2003). Empirical evidence for key hosts in persistence of a tick-borne disease. *International Journal for Parasitology*, *33*, 909–917.
- Pfäffle, M., Littwin, N., Muders, S. V., & Petney, T. N. (2013). The ecology of tick-borne diseases. *International Journal for Parasitology*, *43*, 1059–1077.
- Pucek, Z., Jędrzejewski, W., Jędrzejewska, B., & Pucek, M. (1993). Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica*, *38*, 199.
- Randolph, S. E. (1979). Population regulation in ticks: The role of acquired resistance in natural and unnatural hosts. *Parasitology*, *79*, 141–156.
- Randolph, S. E. (1998). Mighty theories from little acorns grow: Is Lyme disease risk predictable from mast-seeding by oak trees? *Trends in Ecology & Evolution*, *13*, 301–303.
- Randolph, S. E. (2001). The shifting landscape of tick-borne zoonoses: Tick-borne encephalitis and Lyme borreliosis in Europe. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *356*, 1045–1056.
- R Development Core Team. (2013). *R: a language and environment for statistical computing*. Vienna (Austria): R Foundation for Statistical Computing Available from: <http://www.R-project.org>.
- Schauber, E. M., Ostfeld, R. S., & Evans, A. S. (2005). What is the best predictor of annual Lyme disease incidence: Weather, mice, or acorns? *Ecological Applications*, *15*, 575–586.
- Siński, E., Pawelczyk, A., Bajer, A., & Behnke, J. M. (2006). Abundance of wild rodents, ticks and environmental risk of Lyme borreliosis: A longitudinal study in an area of Mazury Lakes district of Poland. *Annals of Agricultural and Environmental Medicine*, *13*, 295–300.
- Stafford, K. C., Cartter, M. L., Magnarelli, L. A., Ertel, S.-H., & Mshar, P. A. (1998). Temporal correlations between tick abundance and prevalence of ticks infected with *Borrelia burgdorferi* and increasing incidence of Lyme disease. *Journal of Clinical Microbiology*, *36*, 1240–1244.
- Szymkowiak, J., & Kuczyński, L. (2015). Avoiding predators in a fluctuating environment: Responses of the wood warbler to pulsed resources. *Behavioral Ecology*, *26*, 601–608.
- Tersago, K., Verhagen, R., Servais, A., Heyman, P., Ducoffre, G., & Leirs, H. (2009). Hantavirus disease (nephropathia epidemica) in Belgium: Effects of tree seed production and climate. *Epidemiology and Infection*, *137*, 250–256.
- Wolff, J. O. (1996). Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy*, *77*, 850–856.
- Zwolak, R., Bogdziewicz, M., & Rychlik, L. (2016). Beech masting modifies the response of rodents to forest management. *Forest Ecology and Management*, *359*, 268–276.
- Żmihorski, M., Dziarska-Pałac, J., Sparks, T. H., & Tryjanowski, P. (2013). Ecological correlates of the popularity of birds and butterflies in Internet information resources. *Oikos*, *122*, 183–190.

Available online at www.sciencedirect.com

ScienceDirect

Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions

Michał Bogdziewicz^{1*}, Elizabeth E. Crone^{2†}, Michael A. Steele³ and Rafał Zwolak¹

¹Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland; ²Harvard Forest, Harvard University, Petersham, MA 01366, USA; and ³Department of Biology, Wilkes University, Wilkes-Barre, PA 18766, USA

Summary

1. Relatively little is known about the effects of anthropogenic environmental changes on reproductive ecology of trees. Yet, recruitment is a primary determinant of the long-term dynamics of plant populations in changing environments.

2. We used the Long-Term Ecological Research site at Harvard Forest to evaluate the effects of chronic (over 25 years) nitrogen fertilization on reproductive ecology of red oaks (*Quercus rubra*).

3. Oaks growing in fertilized plots produced 4–9 times more acorns than control trees. However, nitrogen deposition simultaneously affected oaks' biotic interactions. It increased pre-dispersal seed predation by insects (primarily weevils, *Curculio* spp.) on fertilized plots, most likely as the result of the disruption of predator satiation. In addition, infestation by weevils was more likely to result in embryo destruction in fertilized than in control acorns. Furthermore, the proportion of acorns dispersed and cached by rodents decreased on fertilized plots. Finally, germination of fertilized acorns was lower than control acorns, even after controlling for the effects of weevils and rodents.

4. Inclusion of the altered biotic interactions reversed the final picture of the effects of long-term nitrogen fertilization on oak reproduction: the positive effects on acorn quantity were trumped by the nitrogen-mediated changes in biotic interactions.

5. *Synthesis.* Our results stress the importance of considering indirect effects and consumer interactions when evaluating the effects of environmental change on plant population dynamics. Long-term nitrogen fertilization has a strong potential to decrease the recruitment of masting trees. Given the ubiquitous increase in the anthropogenic nitrogen deposition, processes similar to those found in our system might operate in others, resulting in a widespread alteration in trees' recruitment dynamics.

Key-words: global change, mast seeding, nitrogen fertilization, predator satiation, recruitment, reproductive ecology, seed dispersal, seed predation, seed production, weevils

Introduction

Ongoing environmental changes exert increasing pressure on forests world-wide, and studies of their effects have become a priority for forest ecologists (Bonan 2008). To date, most research on the effects of environmental change on trees have focused on tree growth, carbon sequestration, seedling and tree survival, or phenology in the context of global warming or changes in atmospheric chemistry (CO₂ and other pollutants) (Wallace *et al.* 2007; Thomas *et al.* 2010; Rapp *et al.* 2012; Talhelm *et al.* 2013; Keenan *et al.* 2014; Murdiyarsa

et al. 2015; Fernández-de-Uña *et al.* 2016). Studies of large-scale ecosystem alterations often overlook reproductive ecology of trees, yet long-term changes in reproduction determine whether tree populations can track moving windows of appropriate climate or soil conditions (Richardson *et al.* 2005; Pérez-Ramos *et al.* 2010). Therefore, insufficient information on changes in tree reproduction undermines our ability to predict responses of forests to global changes.

Anthropogenic nitrogen deposition is one of the main dimensions of global change (Vitousek *et al.* 1997). Anthropogenic emission of reactive nitrogen and its deposition in soils have doubled since the 1890s and are projected to double again by 2050 (Galloway *et al.* 2004, 2008). Currently, the amount of anthropogenic nitrogen added to terrestrial ecosystems exceeds the amount provided by all natural

*Correspondence author. E-mail: micbog@amu.edu.pl

†Present address: Department of Biology, Tufts University, 163 Packard Ave, Medford, MA 02155, USA.

sources combined (Galloway *et al.* 2004). This sharp increase in nitrogen availability affects organisms and their interactions (Aber *et al.* 1989; Tylianakis *et al.* 2008). For example, N-fertilization increases tree growth and seed production (Callahan *et al.* 2008; Smaill *et al.* 2011) and can benefit seed dispersal by indirectly affecting behaviour of animal dispersers (Yi *et al.* 2016). In contrast, N-fertilization decreases seedling emergence and survival for a range of tree species (Catovsky & Bazzaz 2002; Patterson *et al.* 2012; Talhelm *et al.* 2013; but see Sefcik, Zak & Ellsworth 2007). Moreover, it alters tissue production and concentration of secondary compounds in plant tissues, which enhances herbivory (Tylianakis *et al.* 2008). Therefore, to understand the final effects of nitrogen deposition on tree reproduction, we need to integrate both direct effects (e.g. on seed quantity and quality) and indirect changes in plant–animal interactions on seed survival and establishment (Tylianakis *et al.* 2008; Kiers *et al.* 2010).

In this study, we evaluated the effects of long-term (>25 years) N-fertilization on reproductive ecology of red oaks (*Quercus rubra*), a tree species that is important economically and provides food resources to dozens of species (Ostfeld & Keesing 2000; McShea *et al.* 2007; Bogdziewicz, Zwolak & Crone 2016). Previous studies suggested that N-fertilization enhances reproduction of large-seeded, masting plants, such as oaks, by boosting their growth, seed production and seed size (Callahan *et al.* 2008; Smaill *et al.* 2011). However, the influence of nitrogen addition on oak reproduction depends not only on its direct impacts on seed production, but also on indirect consequences of changes in the quantity and quality of acorns on interactions with granivores. In this study, we focused on pre-dispersal seed predation by weevils (Coleoptera: Curculionidae) and seed dispersal by rodents. Both groups of organisms exert strong influence on oak reproduction: weevils can destroy up to 70–90% of the entire acorn crop of an individual tree (Crawley & Long 1995; Espelta *et al.* 2008; Lombardo & McCarthy 2008) and small mammals act as key seed dispersers of oak acorns (Steele 2008; Lichti *et al.* 2014) but can easily shift from mutualists to seed predators depending on various environmental conditions (Theimer 2005; Zwolak & Crone 2012).

Past research suggests that N-fertilization should affect both the quantity of seeds produced and their quality as food for granivores. For example, high availability of nitrogen should increase the amount of plant internal resources, leading to higher reproductive output and lower interannual variation of seed production in masting plants (e.g. Kelly & Sork 2002; Tanentzap, Lee & Coomes 2012; Crone & Rapp 2014). Higher resource availability may also lead to increased seed size (see Callahan *et al.* 2008). On the other hand, N-fertilization could lead to a decrease in tannin concentration in red oak acorns, for example, according to the carbon–nutrient balance hypothesis, which maintains that the concentration of carbon-based secondary compounds in plant tissues should decrease in response to increase in nitrogen availability (Stamp 2003).

Similarly, past studies indicate that changes in quantity and quality of acorns are likely to alter oak–animal interactions. Oaks produce large numbers of seeds at irregular intervals (mast seeding; Kelly 1994). One of the best-supported evolutionary explanations of this reproductive strategy is predator satiation (e.g. Janzen 1971; Norton & Kelly 1988; Crawley & Long 1995; Koenig & Knops 2002; Linhart *et al.* 2014); that is, during low mast years low seed production reduces the population of seed predators and high seed production during mast years exceeds the consumption capacity of consumer populations. Increased acorn production might disrupt this mechanism by providing food in non-mast years (McKone, Kelly & Lee 1998). Changes in seed chemical composition would also be likely to affect plant–consumer interactions. Weevil larvae frequently damage only a portion of the seed cotyledon and leave the embryo undamaged, and the infested acorn is still able to germinate (Steele *et al.* 1993; Bonal, Muñoz & Díaz 2007; Muñoz, Bonal & Espelta 2014). Bigger acorns are generally more likely to survive infestation (Bonal, Muñoz & Díaz 2007; Xiao, Harris & Zhang 2007; Muñoz, Bonal & Espelta 2014). Moreover, a higher tannin concentration around the embryo promotes consumption of the acorn basal end, and acorns with lower tannin content would be less likely to survive infestation (predator satiation at the seed level, cf. Bonal, Muñoz & Díaz 2007). Finally, rodents transport and bury seeds in topsoil for later consumption (scatterhoarding), but some cached seeds are never recovered and can germinate (Vander Wall 2010). Buried seeds are protected from other seed predators and escape high density-dependent mortality under the mother tree which benefits plant recruitment (Jansen *et al.* 2012; Johnson *et al.* 2012; Zwolak & Crone 2012). The fate of scatter-hoarded seeds is often determined by one or more seed traits (reviewed in Lichti, Steele & Swihart 2016). For example, larger seeds are cached more often than smaller ones (Theimer 2003; Jansen, Bongers & Hemerik 2004; Steele *et al.* 2014), and high-tannin seeds are often preferred for storage (Wang & Chen 2008; Vander Wall 2010; but see Zhang, Steele & Yi 2013). Thus, depending on the magnitude and the direction of N-effects on acorns traits, nitrogen addition might result in a higher (e.g. due to increased acorn size) or lower proportion (e.g. due to varied tannin concentration) of cached acorns.

Specifically, we measured the effects of chronic N-fertilization on the quantity and quality (tannin concentration and acorn volume) of acorns. We also estimated weevil infestation and probability of embryo survival of weevil-infested seeds. Finally, we measured preference of granivorous rodents for removing, consuming or caching seeds from N-fertilized trees, and the seedling establishment of these seeds. We combine the net effects of these various interactions in a simple algebraic model to predict the net number of established seedlings from N-fertilized and unfertilized trees. Together, these experiments show the potential for the effects of environmental change on oak reproduction, the relative importance of direct effects on acorn production, and indirect effects mediated by seed consumers.

Materials and methods

STUDY LOCATION

Long-term ecological research

The Chronic Nitrogen Amendment Experiment is located at Harvard Forest in Petersham, Massachusetts, USA. This ongoing experiment is located at a site dominated by ~60-year-old red oaks and divided into four experimental (30 × 30 m) treatments that are further divided into 36, 5 × 5 m subplots (Aber *et al.* 1989; Frey *et al.* 2014). Since 1988, six monthly applications of NH₄NO₃ have been applied to the plots during the growing season (Aber *et al.* 1989). Two plots receive 50 kg ha⁻¹ year⁻¹ ('low-N' plots), and one receives 150 kg ha⁻¹ year⁻¹ ('high-N' plot). The low-nitrogen treatment is applied at two plots because sulphur (74 kg ha⁻¹ year⁻¹) was added on one of them for the first 10 years of the experiment. The addition of sulphur was discontinued because no effects were observed (Magill *et al.* 2004).

Acorn tracking and seedling establishment experiments

For acorn tracking and establishment experiments (conducted in 2013–2014, see below), we established four sites in other parts of Harvard Forest. The sites were located in red oak-dominated hardwood forests and spaced 1.25–5 km apart. Rodent live-trapping revealed relatively low abundance of rodents that was similar among the plots (mean no. of captured individuals ± SE: 4 ± 1.27); acorn rain was estimated with seed traps as 8 ± 2 acorns m⁻² (mean per plot ± SE) (Appendix S1 in Supporting Information). Small mammal communities at the study sites were dominated by mice of genus *Peromyscus*. Although not captured, Eastern grey squirrels (*Sciurus carolinensis*) and Eastern chipmunks (*Tamias striatus*) were frequently seen at the sites and recorded with camera traps.

MEASUREMENTS AND EXPERIMENTS

Estimation of acorn production

We estimated acorn production of individual trees in years 2013–2015 by collecting and counting acorns in the interior of the treatment plots (excluding outer subplots) in a 2-m-radius circle centred at each tree trunk at the beginning of October (30 trees in control, 20 in low-N, and 16 in high-N treatments). Acorns were bagged separately according to the tree of origin, transported to the laboratory and refrigerated (4 °C) until further processing.

Acorn traits and weevil predation

In the laboratory, we weighed, measured (width and length) and assessed insect infestation for individual acorns from each treatment group (years 2013–2015, control = 1448 acorns, low N = 674, high N = 875). Based on acorn dimensions, we calculated acorn volume (following procedure of Bonal, Muñoz & Díaz 2007; see Appendix S1 for details). We also calculated the ratio between acorn length and width (as indicator of acorn shape) as acorn shape might influence rodent foraging decisions (Muñoz, Bonal & Espelta 2012). We cut each acorn transversely into a top (basal) and bottom half (apical) and counted all insect larvae in each half (following earlier protocols, for example Steele *et al.* 1993; Bonal, Muñoz & Díaz 2007). In the article, we only report data for *Curculio* larvae because

larvae of other insects (mostly Diptera; Gibson 1971) were present in less than 10% of all acorns. In 2014, we recorded whether the infestation resulted in embryo depredation and scored the estimated amount of cotyledon consumed.

Tannin concentration

A sample of sound acorns ($n = 5–10$) from each tree were combined to make one composite sample per tree for tannin analyses. Previous studies provided evidence for chemical gradients in acorns that promote consumption of the basal end of the acorns (i.e. avoidance of the apical end) by seed predators (Steele *et al.* 1993). We therefore cut each acorn transversely into a top (basal) and bottom half (apical), removed the outer shell and pericarp and analysed the basal and apical halves separately. Two combined samples (each one consisting of either basal or apical halves of the acorns) were then immediately cut into smaller pieces, quick-frozen by immersion in liquid nitrogen, freeze-dried for 96 h and then ground to a fine powder. We analysed tannin concentration using the radial diffusion assay (Hagerman 1987) by calculating tannic acid equivalent (TAE, A. Hagerman, pers. comm.) for two replicate samples for each acorn sample. We analysed tannin concentration in 2013 and 2014 because acorn production in 2015 was too low to obtain sufficient material.

Acorn tracking experiments

To evaluate the effects of nitrogen fertilization on rodent dispersal behaviour, we conducted an acorn tracking experiment. We tracked acorns using the tin tag method (Xiao, Jansen & Zhang 2006). Preparation of acorns consisted of drilling 0.8 mm diameter holes through the basal end of the acorn, inserting and tying a stainless steel wire (120 mm length, 0.2 mm diameter) to the acorn, and attaching a red, uniquely numbered plastic tag (30 × 40 mm) to the terminal end of the wire. All acorns were weighed before the experiments. We placed acorns in enclosures (1 m × 1 m × 0.5 m, 1-cm mesh hardware cloth) with openings on each side to allow rodent access, but exclude other seed predators such as black bears (*Ursus americanus*) (Moore *et al.* 2007). Acorns were floated and visually examined for oviposition holes to determine weevil infestation; only non-infested acorns were used in experiments.

At each site, we deployed four enclosures spaced 100 m from each other. In each enclosure, we presented 15 acorns of each treatment (control, low-N and high-N; 720 acorns in total). We deployed acorns in October 2013 and checked and recorded acorn fates every day for first 10 days and then on the 15th, 30th, just after snowmelt in 2014, and again in July 2014 to determine their final fate. At each check, we recorded acorns that were eaten at the seed station or removed. If removed, we searched around the seed depots in ~20 m radius centred at the depot, with haphazard searches conducted at longer distances. For the acorns we found, we measured the distance from the depot and categorized the fate of the acorn as: (i) consumed, (ii) left on surface, (iii) buried in soil, or (iv) missing. Acorns found on the surface or cached were marked with a stick and their fate was further monitored at each check.

Seedling establishment experiment

To evaluate the effects of nitrogen fertilization on acorn germination, we conducted seed sowing experiments. We sowed non-infested acorns in 18 × 18 cm wire mesh enclosures (mesh size 13 mm). Acorns were buried 2 cm below the soil surface. At each site, we set

out six sets of four enclosures (24 cages per site). Enclosures within each set were spaced ~2 m apart forming a square. The sets were located in 30-m intervals on two transects that were spaced 30 m from each other. We sowed acorns (five per cage) in October 2013. In each set, we sowed control acorns in two enclosures, and in the other two, we sowed randomly low-N or high-N acorns (control = 240 acorns, low N = 120, high N = 120). Established seedlings were determined the following October (i.e. 2014).

The above treatment was crossed with a treatment for rodent exclusion: in half of the enclosures, rodents were excluded and in other half we cut 70 × 70 mm holes to allow access by small mammals. This allowed us to separate the effects of nitrogen-induced changes in seed traits *per se* on the probability of establishment (e.g. establishment lowered by the decline in tannin concentration in acorns; closed cages), from the potential effects of nitrogen fertilization resulting from trait-mediated changes in pilferage rates (e.g. greater retrieval of larger acorns by rodents (Perea *et al.* 2016)).

DATA ANALYSIS

We analysed data using generalized linear mixed models (GLMMs) implemented via 'LME4' package (Bates *et al.* 2015) in R (R Development Core Team 2015). We tested for statistical significance of fixed factors with Wald type II chi-square test. Unless stated otherwise, the degrees of freedom for fixed effects equalled 1. In all models, we arrived to final model structure by removing non-significant interaction terms. The data were deposited in Dryad repository (Bogdziewicz *et al.* 2016).

EFFECTS OF N-FERTILIZATION ON QUANTITY AND QUALITY OF ACORNS

We tested the effects of N-fertilization on the number of acorns produced using a Poisson family, log-link model with tree-level acorn count as the response variable, and nitrogen treatment (control, low-N, high-N), year and treatment × year interaction as fixed effects. We used tree ID as a random effect. We tested whether acorns differed in size among treatments using a Gaussian family, identity link model with acorn volume as the response variable, the treatment and year as fixed effects, and tree ID as the random effect. We also tested for differences in acorn shape (height to width ratio) using a similar model. We tested whether tannin concentration in acorns differed among treatments using a Gaussian family, identity link model with log-transformed TAE as the response variable. This model included nitrogen treatment, acorn part (basal/apical), year, treatment × acorn part and treatment × acorn part × year interactions as fixed effects, and tree ID as a random effect.

EFFECTS OF N-FERTILIZATION ON SEED-CONSUMER INTERACTIONS

We modelled the prevalence of larvae in acorns using a binomial family, logit link model with weevil infestation (0/1) as the response variable, treatment, individual tree crop size, acorn volume, year and interaction terms: treatment × individual tree crop size, treatment × year as fixed effects, and tree ID as a random effect. We also analysed the multi-infestation (i.e. the number of larvae per infested acorn), but it did not differ among treatments (see Appendix S1). We analysed the proportion of cotyledon depredated by weevil larvae using a binomial family, logit link model with the proportion of cotyledon consumed (Zuur *et al.* 2009) (using only acorns infested by

weevils) as the response variable, nitrogen treatment, weevil larvae count, acorn volume, year, and interaction of treatment × volume, treatment × larvae count, and treatment × year as fixed factors, and tree ID as a random effect. To analyse embryo survival of infested seeds, we used a binomial family, logit link model with embryo survival (0/1) as response variable, and the same set of fixed and random effects as in the cotyledon depredation model.

In the rodent-caching experiment, we tested whether the fate of acorns differed among treatments (control, low N, high N) with regard to (i) probability of removal, (ii) probability of consumption, (iii) probability of caching, and (iv) removal distance using four models. For response variables (i)–(iii), we used binomial family, logit link models. For response (iv), removal distance, we used a Gaussian family with log-transformed removal distance and an identity link. Each model included seed station nested within study plot as random effects. Fixed effects included treatment and acorn mass.

To evaluate the effects of N-fertilization on seedling establishment, we tested whether the establishment from experimental caches differed among treatments using a binomial family, logit link model. We compared the establishment of control and N acorns by building a GLMM with treatment (control, low N, high N), rodent access (open vs. closed cages) and the interaction term as fixed effects. Random effects included block (i.e. cages set) nested within study site.

THE NET EFFECT OF NITROGEN FERTILIZATION ON RED OAK REPRODUCTION

As a final step, we combined the results of experiments and calculated the net effect of N-fertilization on the reproductive output of red oaks by building a model:

$$\text{Net} = A_p \times (1 - P_i \times (1 - S_e)) \times P_c \times G_p.$$

In the model, the net reproductive output (Net) equals the number of acorns produced (A_p) reduced by the proportion of acorns infested (P_i), multiplied by the probability that infested acorns do not survive ($1 - S_e$). Of the non-destroyed acorns, a proportion will be dispersed and cached by small mammals (P_c) and finally establish with probability G_p . We used parameter estimates from the above-described GLMMs and obtained standard errors with parametric bootstrapping, that is sampling from the distributions defined by the mean and standard error of each coefficient to obtain a joint distribution for the derived variables.

Results

EFFECTS OF N-FERTILIZATION ON QUANTITY AND QUALITY OF ACORNS

Nitrogen fertilization significantly increased acorn production in red oaks ($\chi^2 = 179.16$, d.f. = 2, $P < 0.001$, Fig. 1). Acorn production was highest at the high-N plot (from 4 to 9 times higher than at the control plot, depending on year; control vs. high N: $\chi^2 = 113.32$, $P < 0.001$; low N vs. high N: $\chi^2 = 76.80$, $P < 0.001$), followed by the low-N plots (2–7 times higher than at the control; control vs. low N: $\chi^2 = 19.59$, $P < 0.001$). The effect of nitrogen fertilization varied by year ($\chi^2 = 35.18$, d.f. = 4, $P < 0.001$): the increase in acorn production in N-fertilized plots relative to the control plot was similar in 2013 and 2014 and weaker in 2015. Acorns produced by oaks growing at fertilized sites were

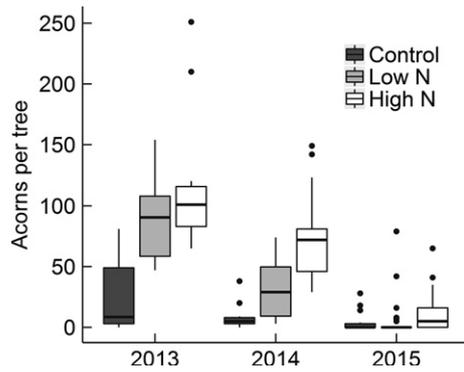


Fig. 1. Acorn production by red oaks in years 2013–2015. ‘Low N’ refers to acorns produced by red oaks growing on plots that were fertilized with $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of reactive nitrogen per year, and ‘high N’ with $150 \text{ kg ha}^{-1} \text{ year}^{-1}$. ‘Control’ refers to oaks growing on plots receiving ambient levels of nitrogen. Boxes denote 25th, 50th and 75th percentiles, whiskers denote the farthest data points within 1.5 interquartile range, and dots denote outliers beyond the 1.5 interquartile range.

smaller than acorns from the control plot (mean \pm SD: control: $75.90 \pm 18.55 \text{ cm}^2$; low N: $57.68 \pm 14.66 \text{ cm}^2$; high N: $65.56 \pm 22.52 \text{ cm}^2$), although the difference between control and high N was non-significant (control vs. low N: $\chi^2 = 22.50$, $P < 0.001$; control vs. high N: $\chi^2 = 2.89$, $P = 0.09$). Acorns of low N were smaller than high-N treatment ($\chi^2 = 21.20$, $P < 0.001$). Moreover, acorns produced by oaks growing on N-fertilized plots were more spherical than control acorns (i.e. had smaller length to width ratio, $\chi^2 = 17.73$, d.f. = 2, $P < 0.001$, Fig. S1).

Overall, nitrogen treatment did not have a significant effect on tannin concentration in acorns ($\chi^2 = 0.84$, d.f. = 2, $P = 0.65$). However, the effect of nitrogen fertilization on tannin concentration differed with acorn part and year (treatment \times acorn part \times year interaction: $\chi^2 = 9.66$, d.f. = 2, $P = 0.007$). When years were analysed separately, fertilization affected tannin concentration in 2013 ($\chi^2 = 7.32$, d.f. = 2, $P = 0.02$), and this effect differed between acorn parts

($\chi^2 = 20.46$, d.f. = 2, $P < 0.001$, Fig. S2). Nonetheless, general effects of nitrogen treatments were similar in basal and apical halves of acorns: low-N acorns had a lower tannin concentration than control acorns in both acorn parts (basal half: $\chi^2 = 10.04$, $P = 0.001$; apical half: $\chi^2 = 3.79$, $P = 0.05$), whereas the difference between control and high-N acorns was not significant (basal half: $\chi^2 = 2.31$, $P = 0.12$; apical half: $\chi^2 = 0.26$, $P = 0.60$). In 2014, we found no effect of nitrogen treatment on tannin concentration ($\chi^2 = 0.03$, d.f. = 2, $P = 0.98$). Generally, tannin concentration was higher in apical than in basal part of the acorns ($\chi^2 = 29.53$, $P < 0.001$).

EFFECTS OF N-FERTILIZATION ON SEED-CONSUMER INTERACTIONS

The overall prevalence of weevil larvae in acorns was 38% in control, 49% in low-N and 59% in high-N acorns (Fig. 2). The probability of acorn infestation increased with acorn volume ($\chi^2 = 16.58$, $P < 0.001$). When controlling for acorn volume, the odds of infestations by weevils were 1.61 times greater for low-N (95% CI: 1.1–2.4) and 2.66 times greater for high-N acorns (95% CI: 1.9–3.8) in comparison with control acorns. These differences were statistically significant (control vs. low N: $\chi^2 = 6.56$, $P = 0.01$; control vs. high N: $\chi^2 = 24.72$, $P < 0.001$; low N vs. high N: $\chi^2 = 6.83$, $P = 0.008$). The prevalence of weevils decreased with increasing acorn production of individual trees ($\chi^2 = 15.14$, $P < 0.001$; Fig. 2). The prevalence did not differ among years ($\chi^2 = 4.88$, d.f. = 2, $P = 0.08$). All interaction terms were non-significant ($P > 0.2$).

The proportion of cotyledon consumed by weevil larvae was ~ 1.5 times higher in N-fertilized acorns (both low and high N) than in control acorns, and decreased with acorn volume ($\chi^2 = 3.40$, $P = 0.05$). When controlling for acorn volume, the proportion of cotyledon consumed was lower in control acorns than in both low-N ($\chi^2 = 9.05$, $P = 0.002$) and high-N acorns ($\chi^2 = 18.22$, $P < 0.001$). It did not differ between low-N and high-N acorns ($\chi^2 = 0.23$, $P = 0.63$).

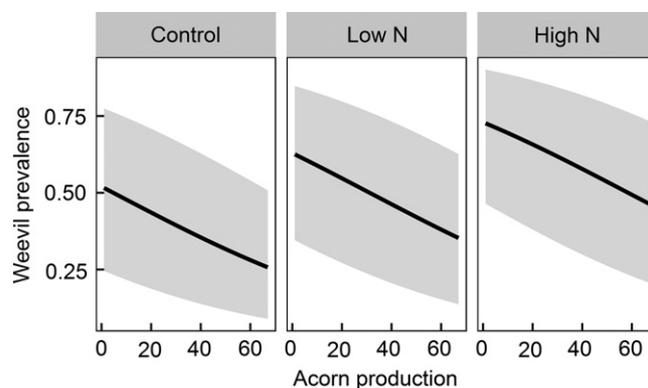


Fig. 2. The proportion of acorns infested by weevil larvae (prevalence) in relation to the tree-level index of acorn production and nitrogen treatment. The estimates are pooled for 2013–2015, because no significant difference was found in infestation among years. Trend lines are reported with 95% confidence intervals and are based on predictions from generalized linear mixed model (see Methods section for details). ‘Low N’ refers to acorns produced by red oaks growing on plots that were fertilized with $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of reactive nitrogen per year, and ‘high-N’ trees were fertilized with $150 \text{ kg ha}^{-1} \text{ year}^{-1}$. Control oaks were grown on plots receiving ambient levels of nitrogen.

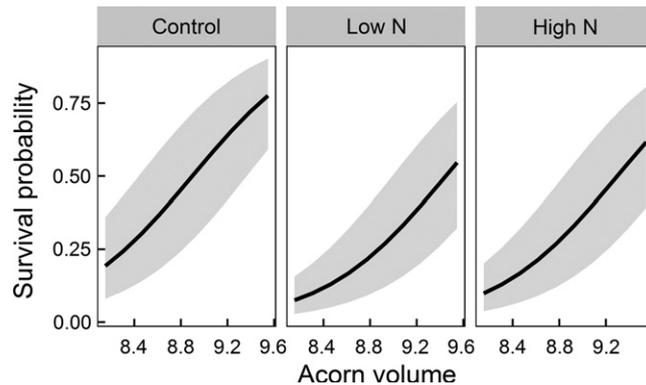


Fig. 3. Survival of embryos of weevil-infested acorns in relation to log-transformed acorn volume and nitrogen treatment. Trend lines are reported with 95% confidence intervals and are based on predictions from generalized linear mixed model (see Methods section for details). ‘Low N’ refers to acorns produced by red oaks growing on plots that were fertilized with 50 kg ha⁻¹ year⁻¹ of reactive nitrogen per year, and ‘high-N’ trees were fertilized with 150 kg ha⁻¹ year⁻¹. Control oaks were grown on plots receiving ambient levels of nitrogen.

None of the interaction terms were significant ($P > 0.40$). Probability of embryo survival in infested acorns increased with acorn volume ($\chi^2 = 10.84$, $P < 0.001$, Fig. 3). After controlling for acorn volume, the odds of acorn survival were 3.03 times higher in control acorns than in low-N acorns ($\chi^2 = 6.80$, $P = 0.009$), and 2.22 times higher in controls than in high-N acorns ($\chi^2 = 4.59$, $P = 0.03$, Fig. 3). The odds of acorn survival did not differ between low-N and high-N acorns ($\chi^2 = 0.32$, $P = 0.56$). None of the interaction terms were significant ($P > 0.15$), and we removed them from the final model.

In the rodent-caching experiment, 46% of all acorns were eaten *in situ*. Predation of control acorns was higher than that of both low-N ($\chi^2 = 6.70$, $P = 0.009$; Fig. S3) and high-N acorns ($\chi^2 = 31.24$, $P < 0.001$). A higher proportion of low-N acorns was consumed *in situ* than that of high-N acorns ($\chi^2 = 11.18$, $P < 0.001$). The probability of *in situ* predation was slightly higher for smaller acorns ($\chi^2 = 3.29$, $P = 0.07$). Eighteen percent of experimental acorns were removed by small mammals. The proportion of removed acorns differed among treatments ($\chi^2 = 19.10$, d.f. = 2, $P < 0.001$) and was positively affected by acorn mass ($\chi^2 = 5.90$, $P = 0.01$). Removal of control acorns (25%) was higher than that of both low-N (17%, $\chi^2 = 4.80$, $P < 0.001$) and high-N acorns (12%, $\chi^2 = 22.14$, $P < 0.001$). High-N and low-N acorns did not differ in removal rates ($\chi^2 = 3.05$, $P = 0.08$).

Fifty-six percent of removed acorns were found consumed and 19% were found cached. Acorn retrieval did not differ between treatments ($\chi^2 = 1.17$, d.f. = 2, $P = 0.56$). The proportion of removed acorns that were consumed did not differ between treatments ($\chi^2 = 1.47$, d.f. = 2, $P = 0.47$) and was not influenced by acorn mass ($\chi^2 = 0.04$, $P = 0.83$). Similarly, caching probability of removed acorns did not differ between treatments ($\chi^2 = 3.74$, d.f. = 2, $P = 0.15$) and was not influenced by acorn mass ($\chi^2 = 0.04$, $P = 0.83$). However, differences in acorn removal resulted in differences in the absolute proportion of cached and non-retrieved acorns ($\chi^2 = 11.37$, d.f. = 2, $P = 0.003$; Fig. S3). A higher proportion of control acorns than that of both low-N and high-N

acorns was cached (control vs. low N: $\chi^2 = 5.76$, $P = 0.016$, control vs. high N: $\chi^2 = 7.45$, $P = 0.006$). Low-N and high-N acorns did not differ in caching probability ($\chi^2 = 0.65$, d.f. = 1, $P = 0.41$). Dispersal distance did not differ among treatments ($\chi^2 = 3.85$, d.f. = 2, $P = 0.14$; Table 1) and was not influenced by acorn mass ($\chi^2 = 0.87$, $P = 0.37$).

In the germination experiment, seedling establishment was higher in control than in both low-N and high-N treatments, both in open and closed cages ($\chi^2 = 29.34$, d.f. = 2, $P < 0.001$; Fig. 4). This effect was stronger when rodents were excluded (nitrogen \times rodent access interaction: $\chi^2 = 8.64$, $P = 0.01$; see Table S1 for all *post hoc* tests). This interaction was driven by a stronger effect of rodent predation on establishment of control acorns in comparison with those from N-treatments (Fig. 4).

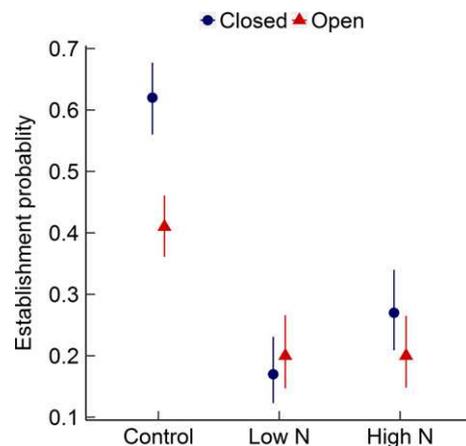


Fig. 4. Probability of seedling establishment of buried acorns. ‘Low N’ refers to acorns produced by red oaks growing on plots that were fertilized with 50 kg ha⁻¹ year⁻¹ of reactive nitrogen per year, and ‘high N’ with 150 kg ha⁻¹ year⁻¹. Control refers to oaks growing on plots receiving ambient levels of nitrogen. *Closed* denotes emergence when rodents were excluded, and *Open* refers to emergence when rodent access was allowed. Dots represent GLMM estimates, and whiskers represent standard errors (for detailed description of the model, see Methods).

THE NET EFFECT OF NITROGEN FERTILIZATION ON RED OAK REPRODUCTION

Strong positive effects of nitrogen fertilization on acorn production were trumped by the negative biotic effects (Fig. 5). Depending on the year, N-fertilization reduced the mean net recruitment by ca. 13–29% (low-N) and by 3–16% (high-N) in comparison with control. The relative reduction in recruitment was more pronounced in the low-N treatment than in the high-N treatment because it was compensated by the stronger increase in acorn production in the latter.

Discussion

We found strong, multilevel effects of long-term N-fertilization on reproductive ecology of red oaks. Nitrogen addition increased acorn production up to nine fold, but simultaneously resulted in higher pre-dispersal seed predation by weevils, decreased caching by rodents and decreased seedling establishment. All these combined effects led to decrease in the net recruitment rate (Table 1). These results point to the importance of considering indirect effects and consumer interactions when evaluating the effects of global changes on tree reproductive ecology; inferences based on acorn quantity alone would lead to the opposite conclusions.

N-FERTILIZATION INCREASES PRE-DISPERSAL ACORN PREDATION

Despite substantial differences in acorn production among years, the proportion of acorns infested by weevils did not change over time (i.e. no effect of predator satiation at the population level). This result contrasts with studies on other species of oaks (e.g. [Crawley & Long 1995](#); [Espelta *et al.* 2008](#)), but is consistent with our observations in the north-eastern USA (relatively constant levels of weevil infestation

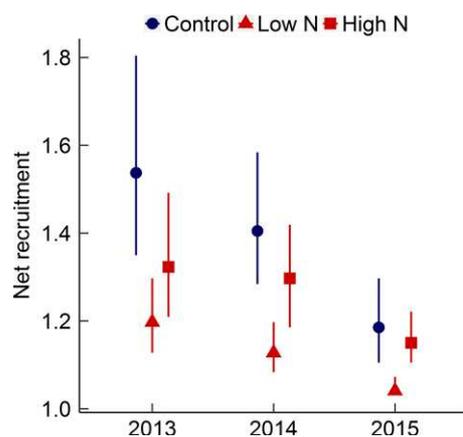


Fig. 5. Estimated net recruitment of red oaks: the number of acorns produced multiplied by weevil pre-dispersal acorn predation, probability of rodent dispersal and acorn germination. Whiskers indicate 95% confidence intervals. 'Low N' refers to acorns produced by red oaks growing on plots that were fertilized with $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ of reactive nitrogen per year, and 'high-N' trees were fertilized with $150 \text{ kg ha}^{-1} \text{ year}^{-1}$. Control oaks were grown on plots receiving ambient levels of nitrogen.

Table 1. Summary of the effects of long-term N-fertilization on the reproductive ecology of red oaks

	Fertilization effect
<i>Quantity and quality of acorns</i>	
Acorn production	Twofold to nine fold increase
Tannin concentration	Decrease in 'low N', in 2013
Acorn size	Decrease
<i>Oak seed–consumers interactions</i>	
Proportion of acorn crop infested by weevils	10–20% increase
Proportion of cotyledon consumed by weevil larvae	20–30% increase
Survival of weevil-infested acorns	Twofold to threefold decrease
Proportion of acorns cached by rodents	Decrease from 6.3% to 1.7% (low N) or 0.008% (high N)
Germination probability	Twofold to threefold decrease
The net effect	3–29% decrease in recruitment

of red oak acorns in a 16-year data set; M. Steele, unpubl. data). Weevils are known to undergo diapause that lasts 2–4 years ([Menu & Debouzie 1993](#); [Venner *et al.* 2011](#)). The diapause may allow weevils to track acorn production and buffer their populations against the negative effects of low mast years ([Kelly *et al.* 2000](#); [Maeto & Ozaki 2003](#)). The tracking is most effective when masting occurs at a predictable cycle, for example in alternate years, and out-of-synchrony lean years severely decrease weevil numbers ([Shibata *et al.* 2002](#); [Maeto & Ozaki 2003](#)). Similarly, two or more lean years in a row severely reduce weevil abundance ([Higaki 2016](#)). Thus, the higher proportion of acorn crop destroyed by weevils at the fertilized sites is likely to be the result of a more stable acorn supply, consequently a higher average survival of weevil cohorts, and a localized build-up of the weevil population ([McKone, Kelly & Lee 1998](#); [Maeto & Ozaki 2003](#); [Higaki 2016](#)). Enhanced seed production induced by global changes was reported for other masting plants (e.g. [Richardson *et al.* 2005](#); [Övergaard, Gemmel & Karlsson 2007](#); [Buechling *et al.* 2016](#)), but the apparent positive effects were treated cautiously because of possible consequences for seed predation ([McKone, Kelly & Lee 1998](#); [Richardson *et al.* 2005](#); [Koenig *et al.* 2015](#)). Our study shows that the enhanced seed production indeed comes with elevated costs.

N-FERTILIZATION REDUCES ACORN DISPERSAL

Reproduction of many large-seeded plant species relies on seeds that are dispersed and buried by scatter-hoarding birds and mammals, but are not recovered under certain conditions ([Theimer 2005](#); [Vander Wall 2010](#); [Jansen *et al.* 2012](#); [Lichti, Steele & Swihart 2016](#); [Pesendorfer *et al.* 2016](#); [Zwolak, Bogdziewicz & Rychlik 2016](#); [Zwolak *et al.* 2016](#)). Nitrogen fertilization decreased the proportion of cached and non-retrieved acorns from 6.3% of controls to 1.7% of low-N acorns, and to only 0.008% of high-N acorns. The differences in caching rates followed from the first step of the seed-handling process ([Wang *et al.* 2013](#)): rodents removed a lower proportion of nitrogen-fertilized than control acorns, but once

acorns were removed, there was no difference in the fates of acorns of different origin. Generally, rodents maximize their energy intake by removing higher energy, larger and lower tannin seeds (Lichti, Steele & Swihart 2016). Acorns of larger size are more likely to be removed and cached (Ivan & Swihart 2000; Steele *et al.* 2014; Lichti, Steele & Swihart 2016), which is consistent with our observation that smaller acorns at N-sites were less likely to be dispersed. Acorns from the 'low-N' site had also lower tannin concentration which also leads to higher rejection rate by rodents (Schmidt, Brown & Morgan 1998; Wang, Wang & Chen 2012; Wang *et al.* 2013). Moreover, acorns at N-sites were more spherical than control acorns, and the shape of acorns affects rodent behaviour as well, likely by affecting the mechanical cost of transport (Muñoz, Bonal & Espelta 2012). Nevertheless, we do not exclude the possibility that the change in rodent behaviour was caused by a nitrogen-induced alternation in chemical composition of acorn cotyledons that remained undetected in this study. In our other experiments, N-fertilization decreased the rate of cotyledon consumption by weevils and decreased seedling establishment of non-infested acorns, suggesting other changes in acorn chemical composition.

Contrary to our results, one other study that examined the effects of N-fertilization on the rodent seed dispersal in Korean pine (*Pinus koraiensis*) found an increase in energy content of seeds and alternation in volatile compounds that led to decreased predation and increased caching of seeds (Yi *et al.* 2016). Thus, the effects of N-fertilization on seed traits are likely to be species specific, which agrees with past studies examining the effects of N-addition on chemical composition of plant tissues (Stamp 2003; Endara & Coley 2011). Seed traits largely determine rodent predation and dispersal that act as strong ecological filters in plant communities (Howe & Brown 2001; Pérez-Ramos *et al.* 2008; Bricker & Maron 2012). Thus, nitrogen-mediated changes in seeds quality might alter preferences of seed predators potentially leading to shifts in composition of plant communities. Studies examining such effects will be a valuable area of future research.

N-FERTILIZATION REDUCES SEEDLING GERMINATION

The decrease in establishment of oak seedlings found in our study is consistent with results from a limited number of previous experiments that found decreases in establishment and survival of tree seedlings in response to N-fertilization (Catovsky & Bazzaz 2002; Patterson *et al.* 2012; BassiriRad *et al.* 2015; but see Sefcik, Zak & Ellsworth 2007). The exact mechanisms of the lowered establishment are currently poorly known (Catovsky & Bazzaz 2002; BassiriRad *et al.* 2015), but in small-seeded trees, such as maples, the lowered establishment follows from increased litter accumulation caused by increased N-deposition (Patterson *et al.* 2012). In other species, including oaks, the lowered establishment and survival is probably caused by the imbalance of above- and below-ground resource allocation (Catovsky & Bazzaz 2002; BassiriRad *et al.* 2015). These effects are unlikely to be compensated at later life stages because N-fertilization increases

browsing damage of oak saplings (Cha *et al.* 2010). Moreover, in adult trees, increased N-deposition increases growth but simultaneously also mortality, leading to a net loss of living basal area (Wallace *et al.* 2007).

CAVEATS AND OTHER POTENTIAL EFFECTS OF N-FERTILIZATION ON OAKS' REPRODUCTIVE ECOLOGY

Some estimates of the N-driven reduction in oak recruitment are likely conservative. For example, we assumed that germination of weevil-infested but not destroyed (i.e. with intact embryos) acorns did not differ among treatments. However, weevils consumed a higher proportion of cotyledons in N-treatments than in control treatments, which will further lower establishment and survival of seedlings because a smaller pool of resources is available for seedling development (Bonal, Muñoz & Díaz 2007; Xiao, Harris & Zhang 2007; Muñoz, Bonal & Espelta 2014). Secondly, we assumed that the dispersal of sound and infested but not destroyed acorns is similar. However, infested acorns are less preferred for caching (Steele, Hadj-Chikh & Hazeltine 1996; Perea, San Miguel & Gil 2011), and the number of infested but non-destroyed acorns was higher in N-treatments. Thirdly, more stable seed production might alter interactions of plants with other consumers. For example, seed production of masting trees determines population dynamics of small mammals and birds and causes aggregation of large-bodied seed predators in mast-rich habitats (Bogdziewicz, Zwolak & Crone 2016). Thus, N-mediated increases in seed production could result in not only more intense seed predation by weevils, but also increased predation by vertebrates.

On the other hand, the number of acorns not harvested by rodents was higher in N-treatment. We assumed uncached acorns do not germinate, which might underestimate the regeneration potential of fertilized oaks. However, the establishment of seedlings of red oaks is extremely low without burial (e.g. surface: 0.3% vs. buried: 86%; Haas & Heske 2005), and in the eastern North American hardwood forests acorns are dispersed and buried almost exclusively by rodents (Steele 2008). Moreover, seed dispersal allows seeds to escape the distance- and density-dependent mortality near the parent plant (Hirsch *et al.* 2012), and increases the likelihood of colonization of habitats favourable for germination and establishment for a number of plant species, including oaks (Steele *et al.* 2014; Yi *et al.* 2013). Therefore, the drop in acorn predation near parent plants caused by nitrogen fertilization is unlikely to counterbalance the decrease in acorn dispersal.

The effects of N-fertilization on plant reproduction are likely to be scale dependent. Contrasting nitrogen with control acorns in our experiment allowed rodents to harvest mostly preferred acorns (here, control). In a world polluted with nitrogen, all plants will be affected, but not all will respond in the same manner (Stamp 2003). Thus, nitrogen-induced changes in seed traits will be species specific (see Yi *et al.* 2016), which might alter preferences of seed consumers and potentially lead to shifts in plant communities (Lichti *et al.*

2014). This effect will likely interact with the effects of N-pollution on understorey vegetation; these have been shown to vary among systems from decline, through no effect, to increase in cover (Thomas *et al.* 1999; Gilliam 2006; Gilliam, Hockenberry & Adams 2006). Decrease in plant cover is likely to decrease rodent abundance (e.g. Malo *et al.* 2012; Zwolak, Bogdziewicz & Rychlik 2016), which could increase caching by increasing *per capita* seed availability (Theimer 2005). Furthermore, rodents prefer to cache seeds in open habitats where the pilferage risk is lower (Muñoz & Bonal 2007, 2011; Steele *et al.* 2015). Both effects could decrease or increase caching rates depending on the scale and the magnitude of the effect. Thus, it would be useful to study these effects in different systems in order to find out whether these could mitigate negative effects of N-fertilization on tree reproduction. Similarly, the LTER experiment is surrounded by a non-treated matrix, which could lead to redistribution of weevils in space. For example, if elevated weevil predation was mostly driven by aggregation of weevils in a N-rich habitat, then larger scale pollution might moderate the increase in pre-dispersal predation rate.

Conclusions

Our research shows that N-fertilization has a strong potential to decrease the recruitment of masting trees. Any positive effects of fertilization on acorn production were eliminated by the N-mediated changes in biotic interactions. Given the ubiquitous increase in the anthropogenic nitrogen deposition (Galloway *et al.* 2004), processes similar to those found in our system might operate in others, resulting in a widespread alteration in trees' recruitment dynamics. For example, oak decline and replacement by other tree species is a well-recognized problem and received significant scientific attention in both North America (Abrams 2003; McShea *et al.* 2007) and Europe (Thomas, Blank & Hartmann 2002). When investigating causes of this decline, researchers focus mostly on changes in climate conditions, disturbance regime and introductions of exotic pathogens and pests that decrease growth and survival of seedling and adult trees (Thomas, Blank & Hartmann 2002; Abrams 2003; McShea *et al.* 2007). Our study documents a different mechanism that can play an equally significant role in this phenomenon: anthropogenic nitrogen addition reduces oak reproduction through its effects on oak-granivore interactions.

Author's contributions

M.B., R.Z., M.S. and E.C. conceived the ideas and designed methodology; M.B. and M.S. collected the data; M.B., R.Z. and E.C. analysed the data; and M.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank referees for their critical comments on the previous version of the manuscript. We thank Harvard Forest for permission to conduct the study. Aleksandra Wróbel, Emma Sass and Lauren Redosh provided assistance during

the field work. Adoption of chemical analyses benefited from past guidance from Anne Hagermann, Edmund W. Stiles (deceased), Johanna P. S. Choo and Amy Bradley. We thank Somiah Almeky, Jarret Colvin, Phillip Esemio, Austin Ford, Shealyn Marino and Aaron Piavis for assistance with chemical analyses and these and numerous other students at Wilkes University for the insect analyses of acorns. The study was supported by Polish National Science Centre 'Harmonia' grant no. 2012/04/M/NZ8/00674 awarded to R.Z., by funds from the Fenner Research Fund of Wilkes University for support of chemical analyses, and by funds from Harvard Forest and Tufts University. M.B. was supported by Polish National Science Centre grant 'Etiuda' no. 2015/16/T/NZ8/00018 and the Foundation for Polish Science scholarship 'Start'. All the experiments were conducted with the IACUC permission no. 13-04-162. Authors declare no conflict of interest.

Data accessibility

Data available from the Dryad Digital Repository <http://datadryad.org/resource/doi:10.5061/dryad.2vk77> (Bogdziewicz *et al.* 2016).

References

- Aber, J.D., Nadelhoffer, K.J., Steudler, P. & Melillo, J.M. (1989) Nitrogen saturation in northern forest ecosystems. *BioScience*, **39**, 378–386.
- Abrams, M.D. (2003) Where has all the white oak gone? *BioScience*, **53**, 927–939.
- BassiriRad, H., Lussenhop, J.F., Sehtiya, H.L. & Borden, K.K. (2015) Nitrogen deposition potentially contributes to oak regeneration failure in the Midwestern temperate forests of the USA. *Oecologia*, **177**, 53–63.
- Bonal, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Bogdziewicz, M., Zwolak, R. & Crone, E.E. (2016) How do vertebrates respond to mast seeding? *Oikos*, **125**, 300–307.
- Bogdziewicz, M., Crone, E.E., Steele, M.A. & Zwolak, R. (2016) Data from: Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Dryad Digital Repository*, <http://datadryad.org/resource/doi:10.5061/dryad.2vk77>
- Bonal, R., Muñoz, A. & Díaz, M. (2007) Satiation of pre-dispersal seed predators: the importance of considering both plant and seed levels. *Evolutionary Ecology*, **21**, 367–380.
- Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.
- Bricker, M. & Maron, J. (2012) Postdispersal seed predation limits the abundance of a long-lived perennial forb (*Lithospermum ruderale*). *Ecology*, **93**, 532–543.
- Buechling, A., Martin, P.H., Canham, C.D., Shepperd, W.D. & Battaglia, M.A. (2016) Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology*, **104**, 1051–1062.
- Callahan, H.S., Del Fierro, K., Patterson, A.E. & Zafar, H. (2008) Impacts of elevated nitrogen inputs on oak reproductive and seed ecology. *Global Change Biology*, **14**, 285–293.
- Catovsky, S. & Bazzaz, F.A. (2002) Nitrogen availability influences regeneration of temperate tree species in the understory seedling bank. *Ecological Applications*, **12**, 1056–1070.
- Cha, D.H., Appel, H.M., Frost, C.J., Schultz, J.C. & Steiner, K.C. (2010) Red oak responses to nitrogen addition depend on herbivory type, tree family, and site. *Forest Ecology and Management*, **259**, 1930–1937.
- Crawley, M. & Long, C. (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *Journal of Ecology*, **83**, 683–696.
- Crone, E.E. & Rapp, J.M. (2014) Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, **1322**, 21–34.
- Endara, M.J. & Coley, P.D. (2011) The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology*, **25**, 389–398.
- Espelta, J.M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. & Retana, J. (2008) Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. *Ecology*, **89**, 805–817.
- Fernández-de-Uña, L., McDowell, N.G., Canellas, I. & Gea-Izquierdo, G. (2016) Disentangling the effect of competition, CO₂ and climate on intrinsic water-use efficiency and tree growth. *Journal of Ecology*, **104**, 678–690.
- Frey, S., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A. *et al.* (2014) Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. *Biogeochemistry*, **121**, 305–316.

- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P. et al. (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry*, **70**, 153–226.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, **320**, 889–892.
- Gibson, L.P. (1971) Insects of bur oak acorns. *Annals of the Entomological Society of America*, **64**, 232–234.
- Gilliam, F.S. (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, **94**, 1176–1191.
- Gilliam, F.S., Hockenberry, A.W. & Adams, M.B. (2006) Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest. *The Journal of the Torrey Botanical Society*, **133**, 240–254.
- Haas, J.P. & Heske, E.J. (2005) Experimental study of the effects of mammalian acorn predators on red oak acorn survival and germination. *Journal of Mammalogy*, **86**, 1015–1021.
- Hagerman, A.E. (1987) Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology*, **13**, 437–449.
- Higaki, M. (2016) Prolonged diapause and seed predation by the acorn weevil, *Curculio robustus*, in relation to masting of the deciduous oak *Quercus acutissima*. *Entomologia Experimentalis et Applicata*, **159**, 338–346.
- Hirsch, B.T., Kays, R., Pereira, V.E. & Jansen, P.A. (2012) Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. *Ecology Letters*, **15**, 1423–1429.
- Howe, H.F. & Brown, J.S. (2001) The ghost of granivory past. *Ecology Letters*, **4**, 371–378.
- Ivan, J.S. & Swihart, R.K. (2000) Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy*, **81**, 549–562.
- Jansen, P.A., Bongers, F. & Hemerik, L. (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs*, **74**, 569–589.
- Jansen, P.A., Hirsch, B.T., Emsens, W.-J., Zamora-Gutierrez, V., Wikelski, M. & Kays, R. (2012) Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 12610–12615.
- Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**, 465–492.
- Johnson, D.J., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012) Conspecific negative density dependence and forest diversity. *Science*, **336**, 904–907.
- Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., Munger, W.J., O'Keefe, J., Schmid, H.P., Wing, I.S., Yang, B. & Richardson, A.D. (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, **4**, 598–604.
- Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, **9**, 465–492.
- Kelly, D. & Sork, V. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**, 427–447.
- Kelly, D., Harrison, A.L., Lee, W.G., Payton, I.J., Wilson, P.R. & Schaubert, E.M. (2000) Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos*, **90**, 477–488.
- Kiers, T.E., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010) Mutualisms in a changing world: an evolutionary perspective. *Ecology Letters*, **13**, 1459–1474.
- Koenig, W.D. & Knops, J.M. (2002) The behavioral ecology of masting in oaks. *Oak Forest Ecosystems* (eds W.J. McShea & W.M. Healy), pp. 129–148. The Johns Hopkins University Press, Baltimore, MD, USA.
- Koenig, W.D., Knops, J.M., Carmen, W.J. & Pearse, I.S. (2015) What drives masting? The phenological synchrony hypothesis. *Ecology*, **96**, 184–192.
- Lichti, N.I., Steele, M.A. & Swihart, R.K. (2016) Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews*. doi:10.1111/brv.12240. [Epub ahead of print].
- Lichti, N.I., Steele, M.A., Zhang, H. & Swihart, R.K. (2014) Mast species composition alters seed fate in North American rodent-dispersed hardwoods. *Ecology*, **95**, 1746–1758.
- Linhart, Y.B., Moreira, X., Snyder, M.A. & Mooney, K.A. (2014) Variability in seed cone production and functional response of seed predators to seed cone availability: support for the predator satiation hypothesis. *Journal of Ecology*, **102**, 576–583.
- Lombardo, J.A. & McCarthy, B.C. (2008) Silvicultural treatment effects on oak seed production and predation by acorn weevils in southeastern Ohio. *Forest Ecology and Management*, **255**, 2566–2576.
- Maeto, K. & Ozaki, K. (2003) Prolonged diapause of specialist seed-feeders makes predator satiation unstable in masting of *Quercus crispula*. *Oecologia*, **137**, 392–398.
- Magill, A.H., Aber, J.D., Currie, W.S., Nadelhoffer, K.J., Martin, M.E., McDowell, W.H., Melilo, J.M. & Steudler, P. (2004) Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, **196**, 7–28.
- Malo, A.F., Godsall, B., Prebble, C., Grange, Z., McCandless, S., Taylor, A. & Coulson, T. (2012) Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behavioral Ecology*, **24**, 759–767.
- McKone, M.J., Kelly, D. & Lee, W.G. (1998) Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology*, **4**, 591–596.
- McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D. & Waldon, J. (2007) Forestry matters: decline of oaks will impact wildlife in hardwood forests. *Journal of Wildlife Management*, **71**, 1717–1728.
- Menu, F. & Debouzie, D. (1993) Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae). *Oecologia*, **93**, 367–373.
- Moore, J.E., McEuen, A.B., Swihart, R.K., Contreras, T.A. & Steele, M.A. (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology*, **88**, 2529–2540.
- Muñoz, A. & Bonal, R. (2007) Rodents change acorn dispersal behaviour in response to ungulate presence. *Oikos*, **116**, 1631–1638.
- Muñoz, A. & Bonal, R. (2011) Linking seed dispersal to cache protection strategies. *Journal of Ecology*, **99**, 1016–1025.
- Muñoz, A., Bonal, R. & Espelta, J.M. (2012) Responses of a scatter-hoarding rodent to seed morphology: links between seed choices and seed variability. *Animal Behaviour*, **84**, 1435–1442.
- Muñoz, A., Bonal, R. & Espelta, J.M. (2014) Acorn–weevil interactions in a mixed-oak forest: outcomes for larval growth and plant recruitment. *Forest Ecology and Management*, **322**, 98–105.
- Murdiyarso, D., Purbopuspito, J., Kauffman, J.B., Warren, M.W., Sasmito, S.D., Donato, D.C., Manuri, S., Krisnawati, H., Taberima, S. & Kurnianto, S. (2015) The potential of Indonesian mangrove forests for global climate change mitigation. *Nature Climate Change*, **5**, 1089–1092.
- Norton, D.A. & Kelly, D. (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology*, **2**, 399–408.
- Ostfeld, R.S. & Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, **15**, 232–237.
- Övergård, R., Gemmel, P. & Karlsson, M. (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry*, **80**, 555–565.
- Patterson, S.L., Zak, D.R., Burton, A.J., Talhelm, A.F. & Pregitzer, K.S. (2012) Simulated N deposition negatively impacts sugar maple regeneration in a northern hardwood ecosystem. *Journal of Applied Ecology*, **49**, 155–163.
- Perea, R., San Miguel, A. & Gil, L. (2011) Leftovers in seed dispersal: ecological implications of partial seed consumption for oak regeneration. *Journal of Ecology*, **99**, 194–201.
- Perea, R., Dirzo, R., San Miguel, A. & Gil, L. (2016) Post-dispersal seed recovery by animals: is it a plant- or an animal-driven process? *Oikos*, **125**, 1203–1210.
- Pérez-Ramos, I.M., Urbiet, I.R., Marañón, T., Zavala, M.A. & Kobe, R.K. (2008) Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. *Oikos*, **117**, 1386–1396.
- Pérez-Ramos, I.M., Ourcival, J.M., Limousin, J.M. & Rambal, S. (2010) Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*, **91**, 3057–3068.
- Pesendorfer, M.B., Sillett, T.S., Morrison, S.A. & Kamil, A.C. (2016) Context-dependent seed dispersal by a scatter-hoarding corvid. *Journal of Animal Ecology*, **85**, 798–805.
- R Development Core Team (2015) R: A Language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rapp, J.M., Silman, M.R., Clark, J.S., Girardin, C.A., Galiano, D. & Tito, R. (2012) Intra- and interspecific tree growth across a long altitudinal gradient in the Peruvian Andes. *Ecology*, **93**, 2061–2072.
- Richardson, S.J., Allen, R.B., Whitehead, D., Carswell, F.E., Ruscoe, W.A. & Platt, K.H. (2005) Climate and net carbon availability determine temporal patterns of seed production by Nothofagus. *Ecology*, **86**, 972–981.
- Schmidt, K.A., Brown, J.S. & Morgan, R.A. (1998) Plant defenses as complementary resources: a test with squirrels. *Oikos*, **81**, 130–142.
- Sefcik, L.T., Zak, D.R. & Ellsworth, D.S. (2007) Seedling survival in a northern temperate forest understory is increased by elevated atmospheric carbon dioxide and atmospheric nitrogen deposition. *Global Change Biology*, **13**, 132–146.

- Shibata, M., Tanaka, H., Iida, S., Abe, S., Masaki, T., Niyama, K. & Nakashizuka, T. (2002) Synchronized annual seed production by 16 principal tree species in a temperate deciduous forest, Japan. *Ecology*, **83**, 1727–1742.
- Smaill, S.J., Clinton, P.W., Allen, R.B. & Davis, M.R. (2011) Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, **99**, 870–877.
- Stamp, N. (2003) Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology*, **78**, 23–55.
- Steele, M.A. (2008) Evolutionary interactions between tree squirrels and trees: a review and synthesis. *Current Science*, **95**, 871–876.
- Steele, M.A., Hadj-Chikh, L.Z. & Hazeltine, J. (1996) Caching and feeding decisions by *Sciurus carolinensis*: responses to weevil-infested acorns. *Journal of Mammalogy*, **77**, 305–314.
- Steele, M.A., Knowles, T., Bridle, K. & Simms, E.L. (1993) Tannins and partial consumption of acorns: implications for dispersal of oaks by seed predators. *American Midland Naturalist*, **130**, 229–238.
- Steele, M.A., Contreras, T.A., Hadj-Chikh, L.Z., Agosta, S.J., Smallwood, P.D. & Tomlinson, C.N. (2014) Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behavioral Ecology*, **25**, 206–215.
- Steele, M.A., Rompre, G., Stratford, J.A., Zhang, H., Suchocki, M. & Marino, S. (2015) Scatterhoarding rodents favor higher predation risks for cache sites: the potential for predators to influence the seed dispersal process. *Integrative Zoology*, **10**, 257–266.
- Talhelm, A.F., Burton, A.J., Pregitzer, K.S. & Campione, M.A. (2013) Chronic nitrogen deposition reduces the abundance of dominant forest understorey and groundcover species. *Forest Ecology and Management*, **293**, 39–48.
- Tanentzap, A.J., Lee, W.G. & Coomes, D.A. (2012) Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses. *Ecology*, **93**, 462–469.
- Theimer, T.C. (2003) Intraspecific variation in seed size affects scatterhoarding behaviour of an Australian tropical rain-forest rodent. *Journal of Tropical Ecology*, **19**, 95–98.
- Theimer, T.C. (2005) Rodent scatterhoarders as conditional mutualists. *Seed Fate, Predation, Dispersal and Seedling Establishment* (eds P.M. Forget *et al.*), pp. 283–295. CABI Publishing, Wallingford, UK.
- Thomas, F.M., Blank, R. & Hartmann, G. (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology*, **32**, 277–307.
- Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A. & Austin, K.A. (1999) Plant diversity in managed forests: understorey responses to thinning and fertilization. *Ecological Applications*, **9**, 864–879.
- Thomas, R.Q., Canham, C.D., Weathers, K.C. & Goodale, C.L. (2010) Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience*, **3**, 13–17.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Vander Wall, S.B. (2010) How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 989–997.
- Venner, S., Pélisson, P.-F., Bel-Venner, M.-C., Débias, F., Rajon, E. & Menu, F. (2011) Coexistence of insect species competing for a pulsed resource: toward a unified theory of biodiversity in fluctuating environments. *PLoS ONE*, **6**, 1–9.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Wallace, Z.P., Lovett, G.M., Hart, J.E. & Machona, B. (2007) Effects of nitrogen saturation on tree growth and death in a mixed-oak forest. *Forest Ecology and Management*, **243**, 210–218.
- Wang, B. & Chen, J. (2008) Tannin concentration enhances seed caching by scatter-hoarding rodents: an experiment using artificial 'seeds'. *Acta Oecologica*, **34**, 379–385.
- Wang, B., Wang, G. & Chen, J. (2012) Scatter-hoarding rodents use different foraging strategies for seeds from different plant species. *Plant Ecology*, **213**, 1329–1336.
- Wang, B., Ye, C.X., Cannon, C.H. & Chen, J. (2013) Dissecting the decision making process of scatter-hoarding rodents. *Oikos*, **122**, 1027–1034.
- Xiao, Z., Harris, M.K. & Zhang, Z. (2007) Acorn defenses to herbivory from insects: implications for the joint evolution of resistance, tolerance and escape. *Forest Ecology and Management*, **238**, 302–308.
- Xiao, Z., Jansen, P.A. & Zhang, Z. (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management*, **223**, 18–23.
- Yi, X., Liu, G., Steele, M.A., Shen, Z. & Liu, C. (2013) Directed seed dispersal by a scatter-hoarding rodent: the effects of soil water content. *Animal Behaviour*, **86**, 851–857.
- Yi, X., Li, J., Zhang, M., Zhang, D. & Wang, Z. (2016) Short-term acute nitrogen deposition alters the interaction between Korean pine seeds and food hoarding rodents. *Forest Ecology and Management*, **367**, 80–85.
- Zhang, M., Steele, M.A. & Yi, X. (2013) Reconsidering the effects of tannin on seed dispersal by rodents: evidence from enclosure and field experiments with artificial seeds. *Behavioural Processes*, **100**, 200–207.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health*. Springer Science, New York, NY, USA.
- Zwolak, R., Bogdziewicz, M. & Rychlik, L. (2016) Beech masting modifies the response of rodents to forest management. *Forest Ecology and Management*, **359**, 268–276.
- Zwolak, R. & Crone, E.E. (2012) Quantifying the outcome of plant-granivore interactions. *Oikos*, **121**, 20–27.
- Zwolak, R., Bogdziewicz, M., Wróbel, A. & Crone, E.E. (2016) Advantages of masting in European beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, **180**, 749–758.

Received 7 July 2016; accepted 12 September 2016

Handling Editor: Nicole Rafferty

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supporting information on data collection, analysis, figures, and table.

Table S1. The results of post-hoc comparisons of probability of seedling establishment among treatments.

Fig. S1. Shape of acorns expressed as length to width ratio produced by red oaks receiving different fertilizer treatments.

Fig. S2. Tannin acid concentration expressed as tannin acid equivalent in acorns produced by red oaks receiving different fertilizer treatments in 2013.

Fig. S3. Diagram of acorn fates in seed tracking experiment.

1 Supplementary material, Bogdziewicz *et al.* (2016) Effects of nitrogen deposition on
2 reproduction in a mast tree: benefits of higher seed production are trumped by negative
3 biotic interactions. *Journal of Ecology*

4 **Acorn volume calculation**

5 We have calculated the acorn volume following simplified Bonal, Muñoz & Díaz (2007)
6 procedure, using following term:

$$Volume = \left(\pi L \left(\frac{W}{2} \right)^2 \right) * \left(\frac{L}{W} \right)$$

7 The first term is the volume of cylindrical acorns, and the second term is correction for acorn
8 shape.

9

10 **Multi-infestation**

11 We modeled multi-infestation (*i.e.*, the number of larvae per infested acorn) using a Poisson
12 family, log link model with weevil larvae count as a response variable, treatment, individual
13 tree crop size, acorn volume, acorn part (basal/apical), year, and interaction terms: treatment ×
14 year, treatment × acorn part as fixed effects, and tree ID as a random effect.

15 Multi-infestation did not differ between treatments (mean ± SD: 1.82 ± 1.29; $\chi^2 = 4.81$, df = 2,
16 p = 0.09).

17

18 **Small mammal trapping and acorn fall estimation**

19 **Methods**

20 At each site we established small mammal trapping grid with 49 Sherman live-traps spaced 10
21 m from each other (7 x 7 rows). We conducted trapping at the end August 2013 (the year of
22 seed tracking experiment) for 5 consecutive nights. We baited traps with oats and sunflower
23 seeds and checked every day at morning (08:00) and evening (20:00). We identified each

24 capture to species, marked each with an uniquely-numbered ear tag, and then released it at the
25 place of capture. Trapping was done with IACUC permission #13-04-162.

26 To measure seed fall, we set 20 seed traps on each site (80 in total). Traps were
27 constructed of plastic containers (52.7 x 36.8 x 40 cm) covered with mesh wire and placed on
28 1.2 m wooden poles. We distributed traps in a stratified random design. We used small
29 mammal trapping grid as reference and divided each site into grid of twelve 30 x 20 m
30 rectangles. Each rectangle contained 6 points spaced 10m apart. We then draw two random
31 points within each rectangle and located seed traps there. Two random rectangles were left
32 without traps. We set traps in the 3rd week of August 2013 and checked every week until no
33 acorns were retrieved (middle of November). Collected acorns were bagged, transported to
34 the laboratory, divided into categories (sound, infested, underdeveloped), and counted.

35

36 Results

37 We captured (mean \pm SE) 4 ± 1.2 individuals of *Peromyscus* sp. per site. No other species of
38 rodents were captured. However, we observed grey squirrels *Sciurus carolinensis* and
39 chipmunks *Tamias* sp. on multiple occasions. Estimated acorn fall was 7.92 ± 2.11 acorns per
40 m^2 .

41

42

43

44

45

46

47

48

49

50 **Table S1.** The results of post-hoc comparisons of probability of seedling establishment among
 51 treatments. Seedling establishment in control plots was higher than in nitrogen treatments in
 52 all comparisons. “Low N” refers to acorns produced by red oaks growing on plots that were
 53 fertilized with 50 kg ha⁻¹ yr⁻¹ of reactive nitrogen per year, and “High N” with 150 kg ha⁻¹ yr⁻¹
 54 ¹. In the experiment, nitrogen treatment was crossed with rodent exclusion. *Closed* denotes
 55 seedling emergence when rodents were excluded and *Open* refers to emergence when rodent
 56 access was allowed. The statistics were obtained with GLMM model (see Methods for
 57 details); we tested for statistical significance using Wald chisquare test.

Rodent	Closed			Open		
access:						
Nitrogen	Control vs.	Control vs.	Low N vs.	Control vs.	Control vs.	Low N vs.
treatment:	Low N	High N	High N	Low N	High N	High N
Statistics:	$\chi^2 = 26.59,$ p < 0.001	$\chi^2 = 15.83,$ p < 0.001	$\chi^2 = 1.12, p$ = 0.28	$\chi^2 = 5.89,$ p = 0.01	$\chi^2 = 7.23,$ p = 0.007	$\chi^2 = 0.03,$ p = 0.85

58

59

60

61

62

63

64

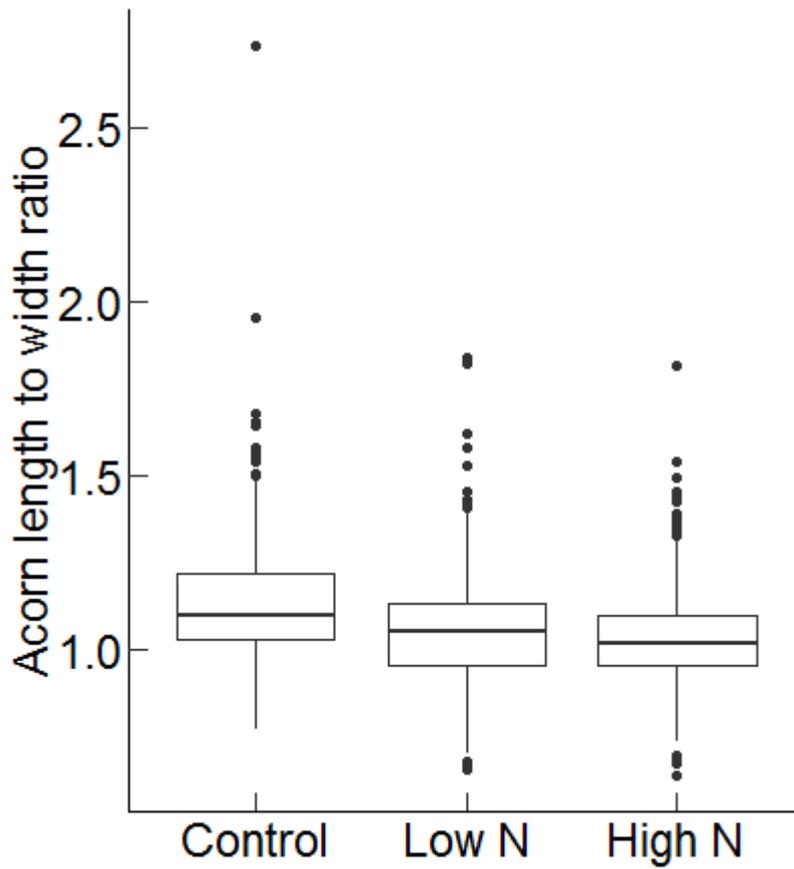
65

66

67

68

69 Figure S1.



70

71 Figure S1. Shape of acorns expressed as length to width ratio produced by red oaks receiving
72 different fertilizer treatments. “Low N” refers to acorns produced by red oaks growing on
73 plots that were fertilized with $50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of reactive nitrogen per year, and “High N” with
74 $150 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Control refers to oaks growing on plots receiving ambient levels of nitrogen.

75

76

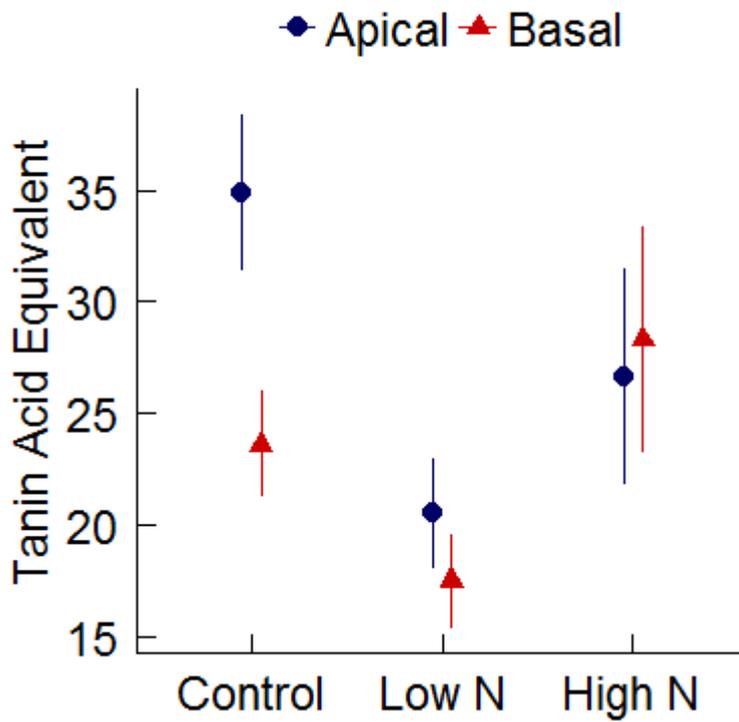
77

78

79

80

81 Figure S2.



82

83

84 Fig. S2. Tannin acid concentration expressed as tannin acid equivalent in acorns produced by
85 red oaks receiving different fertilizer treatments in 2013. No differences among N-treatments
86 were found in 2014 (not shown, see Results). Dots represent GLMM estimates and whiskers
87 represent standard errors (for detailed description of the model see Methods). “Low N” refers
88 to acorns produced by red oaks growing on plots that were fertilized with $50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of
89 reactive nitrogen per year, and “High N” with $150 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Control refers to oaks growing
90 on plots receiving ambient levels of nitrogen.

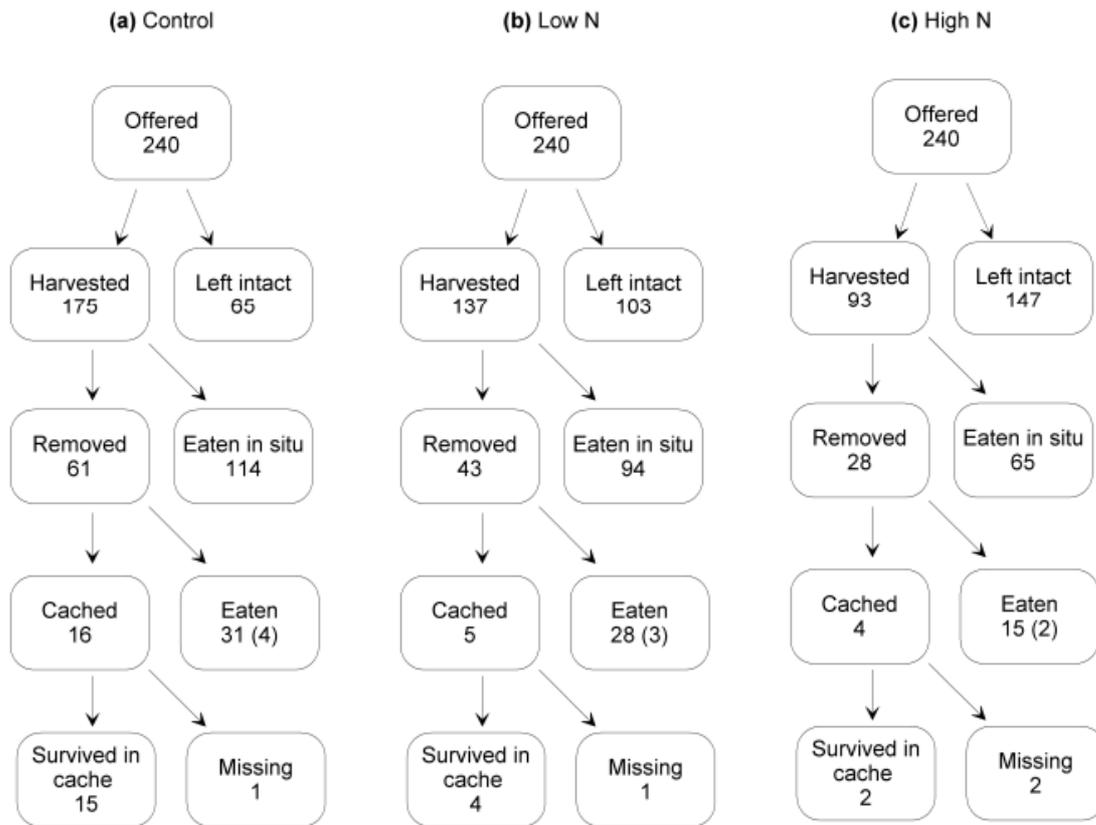
91

92

93

94

95 Figure S3.



96

97 Fig. S3. Diagram of acorn fates in seed tracking experiment. We used 240 acorns in each
 98 treatment (720 in total). “Low N” refers to acorns produced by red oaks growing on plots that
 99 were fertilized with 50 kg ha⁻¹ yr⁻¹ of reactive nitrogen per year, and “High N” with 150 kg
 100 ha⁻¹ yr⁻¹. Control refers to oaks growing on plots receiving ambient levels of nitrogen.
 101 Numbers in parentheses in the ‘eaten’ category represents number of acorns initially left on
 102 the litter surface that were eventually consumed.

103

104

105

IV. Authorship statements

Authorship statements of PhD candidate

1. Bogdziewicz M., Zwolak R., Crone E.E. 2016. How do vertebrates respond to mast seeding? *Oikos* 125:300-307

The role of PhD candidate: first and corresponding author

Contribution (80%):

- Designing the study
- Collecting the data
- Data analysis
- Interpretation of results
- Writing the first draft of the manuscript
- Revising the manuscript

2. Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology & Evolution*, in press

The role of PhD candidate: first and corresponding author

Contribution (60%):

- Designing the study
- Collecting the data
- Data analysis
- Interpretation of results
- Writing the first draft of the manuscript
- Revising the manuscript

3. Bogdziewicz M., Szymkowiak J. 2016. Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe. *Basic & Applied Ecology* 17:300-307

The role of PhD candidate: first and corresponding author

Contribution (70%):

- Designing the study
 - Interpretation of results
 - Writing the first draft of the manuscript
 - Revising the manuscript
4. Bogdziewicz M., Crone E.E., Steele M.A., Zwolak R. 2016. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, in press

The role of PhD candidate: first and corresponding author

Contribution (70%):

- Designing the study
- Collecting the data
- Data analysis
- Interpretation of results
- Writing the first draft of the manuscript
- Revising the manuscript

Poznań, 30.09.2016



Michał Bogdziewicz, MSc
Department of Systematic Zoology
Adam Mickiewicz University

Authorship statements of co-authors of the “How do vertebrates respond to mast seeding?” article.

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Crone E.E. 2016.
How do vertebrates respond to mast seeding? *Oikos* 125:300-307.

I declare that my contribution (10%) to this paper included help in designing the study, analyzing data, and writing and revising the manuscript.

As the supervisor, I confirm that Michał Bogdziewicz had a major contribution (80%) to this study and was a leading author.



Poznań, 30.09.2016

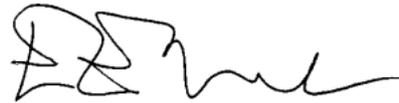
Dr. hab. Rafał Zwolak

Department of Systematic Zoology
Adam Mickiewicz University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Crone E.E. 2016.
How do vertebrates respond to mast seeding? *Oikos* 125:300-307.

I declare that my contribution (10%) to this paper included help in designing the study,
analyzing data, and writing and revising the manuscript.



Poznań, 30.09.2016

Prof. Dr. Elizabeth E. Crone

Department of Biology

Tufts University

Authorship statements of co-authors of the “Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle” article.

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. Ecology & Evolution, in press

I declare that my contribution (10%) to this paper included help in designing the study, collecting the data, and writing and revising the manuscript.

As the supervisor, I confirm that Michał Bogdziewicz had a major contribution (60%) to this study and was a leading author.



Poznań, 30.09.2016

Dr. hab. Rafał Zwolak

Department of Systematic Zoology

Adam Mickiewicz University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology & Evolution*, in press

I declare that my contribution (10%) to this paper included help in analyzing the data, and revising the manuscript.

A handwritten signature in black ink, appearing to read 'LR', with a stylized, cursive flourish extending to the right.

Poznań, 30.09.2016

Lauren Redosh

Department of Biology

Tufts University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology & Evolution*, in press

I declare that my contribution (10%) to this paper included help in collecting the data, and revising the manuscript.



Poznań, 30.09.2016

Prof. Dr. hab. Leszek Rychlik

Department of Biology

Tufts University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Zwolak R., Redosh L., Rychlik L., Crone E.E. 2016. Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology & Evolution*, in press

I declare that my contribution (10%) to this paper included help in designing the study, analyzing the data, and writing and revising the manuscript.



Poznań, 30.09.2016

Prof. Dr. Elizabeth E. Crone

Department of Biology

Tufts University

Authorship statements of co-authors of the “Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe” article.

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Szymkowiak J. 2016. Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe. *Basic & Applied Ecology* 17:300-307

I declare that my contribution (30%) to this paper included help in designing the study, collecting the data, analyzing the data, interpreting the results, and writing and revising the manuscript.



Poznań, 30.09.2016

Dr. Jakub Szymkowiak

Population Ecology Laboratory

Adam Mickiewicz University

Authorship statements of co-authors of the “Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions” article.

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Crone E.E., Steele M.A., Zwolak R. 2016. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. Journal of Ecology, in press

I declare that my contribution (10%) to this paper included help in designing the study, analyzing the data, and writing and revising the manuscript.



Poznań, 30.09.2016

Prof. Dr. Elizabeth E. Crone

Department of Biology

Tufts University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Crone E.E., Steele M.A., Zwolak R. 2016. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. Journal of Ecology, in press

I declare that my contribution (10%) to this paper included help in designing the study, collecting the data, and writing and revising the manuscript.



Poznań, 30.09.2016

Prof. Dr. Michael A. Steele

Department of Biology

Wilkes University

AUTHORSHIP STATEMENT

I confirm that I am co-author of the paper: Bogdziewicz M., Crone E.E., Steele M.A., Zwolak R. 2016. Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. Journal of Ecology, in press

I declare that my contribution (10%) to this paper included help in designing the study, collecting the data, analyzing the data, interpreting results, and writing and revising the manuscript.

As the supervisor, I confirm that Michał Bogdziewicz had a major contribution (70%) to this study and was a leading author.



Poznań, 30.09.2016

Dr. hab. Rafał Zwolak

Department of Systematic Zoology
Adam Mickiewicz University

VII. Acknowledgements/Podziękowania

Niniejsza praca nie mogłaby powstać bez ogromnego merytorycznego i przyjacielskiego wsparcia dra hab. Rafała Zwolaka. Dziękuję za umożliwienie mi prowadzenia badań w najbardziej komfortowych warunkach jakie mógłbym sobie wyobrazić, wszystkie cenne wskazówki i niezłomną cierpliwość. Dzięki Rafał!

I thank prof. Elizabeth E. Crone for her critical and invaluable comments on data analysis and writing, and for her infinite enthusiasm for all my (better and worse) research ideas. I owe you a lot, Elizabeth!

I thank prof. Michael A. Steele for his help with analysis of weevil infestation in red oaks, analysis of chemical content of acorns, and tips on the study design. The research done in this thesis would be not possible without this large support.

Dziękuję prof. Leszkowi Rychlikowi za ciągłe czuwanie nad powodzeniem tego projektu oraz osobiste zaangażowanie w postępy pracy.

Moja żona, Agnieszka Amborska-Bogdziewicz, zapewniła mi niezbędną atmosferę i wsparcie, bez których ukończenie tego doktoratu nie byłoby możliwe. Dzielnie znosiła moje pomysły na alternatywne życie zawodowe w chwilach zwątpienia, oraz z uwagą wysłuchiwała nieskładnych opowiadań o kolejnych pomysłach badawczych. Dziękuję za wspólne cieszenie się z najmniejszego sukcesu, pocieszenie przy potknięciach i super stronę internetową. Kocham Cię 😊

Szczególne podziękowania dla moich rodziców, Anny i Bogusława Bogdziewicz, za ich niekończące się wsparcie, zarówno emocjonalne jak i finansowe, bez których moje studia licencjackie, magisterskie i doktoranckie nie byłyby możliwe. Życzę wszystkim dzieciom świata takich rodziców.

Dziękuję Jakubowi Szymkowiakowi i Krzysztofowi Zawierusze za przyjaźń, naukowe (i poza naukowe) dyskusje, posiedzenia przy piwie i wspólne pokonywanie biurokratycznych problemów. Jakubowi szczególne dzięki za szybkie i skuteczne przejście z pomysłu na połączenie lat nasiennych z boreliozą do zaakceptowania ostatnich poprawek manuskryptu. Nie sądzę, żeby udało mi się jeszcze kiedyś osiągnąć podobne tempo pracy (tak, tak to wyzwanie) 😊.

Dziękuję wszystkim, którzy pomogli w trudnych pracach terenowych, szczególnie Aleksandrze Wróbel, Emmie Sash i Lauren Redosh.

Poznań, listopad 2016

Finansowanie badań

Badania, których wyniki przedstawiono w niniejszej rozprawie zostały sfinansowane przez Narodowe Centrum Nauki (grant HARMONIA nr. 2012/04/M/NZ8/00674, oraz ETIUDA nr. 2015/16/T/NZ8/00018). W czasie studiów doktoranckich korzystałem też ze wsparcia finansowego w postaci stypendium Fundacji UAM, stypendium za wybitne osiągnięcia dla doktorantów Ministerstwa Nauki i Szkolnictwa Wyższego, oraz stypendium dla wybitnych młodych naukowców Fundacji na Rzecz Nauki Polskiej START.