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Is fern endozoochory widespread among fern-eating herbivores?

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Abstract Endozoochory is an important dispersal mechanism for seed plants and has recently been demonstrated to occur also in spore plants, such as ferns, which are commonly consumed by herbivores. However, it is not known whether fern species from particular habitats are differentially preferred by herbivores and whether their spores differ in their ability to survive the gut passage of herbivores. Such differences would suggest adaptation to endozoochorous dispersal, as it is known for seed plants. Moreover, it is unclear whether herbivore species differ in their efficiency to disperse fern spores. In a factorial experiment, we fed fertile leaflets of 13 fern species from different forest and open habitats to three polyphagous herbivore species and recorded the germination of spores from feces after 46 and 81 days. Fern spores germinated in 66 % of all samples after 46 days. At this stage, germination success differed among fern and herbivore species, but was independent of the ferns' habitat. Interestingly, after 81 days fern spores germinated in 85 % of all samples and earlier significant differences in germination success among fern and herbivore species were not sustained.

The overall high germination success and the absence of differences among fern species from different habitats together with the consistency across three tested herbivores strongly imply endozoochorous dispersal to be a taxonomically widespread phenomenon among fern-eating herbivores, which all might act as potential dispersal vectors.

Keywords Dispersal · Invertebrate · Mutualism · Plant-animal interaction · Pteridophyta · Spore germination

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Introduction

Plants exhibit a diverse array of adaptations and strategies to cope with the negative effects of herbivorous animals (Crawley 1983; Walling 2000; Lind et al. 2013). In some instances, these negative effects may even be offset by the evolution of mutualistic interactions with herbivores (e.g., over compensation sensu Paige and Whitham 1987). One example of an evolved mutualistic plant–herbivore relationship is endozoochory, which comprises the dispersal of propagules inside animals after consumption. Endozoochory is of particular importance for plants due to their immobility and may vary among habitats relative to differences in herbivory pressure (Cousens et al. 2008). Gut passage of propagules often changes seed traits such as an increased permeability of the seed

coat resulting in a higher germination rate (e.g., Traveset et al. 2008). There is a wealth of case studies on propagule dispersal of seed plants and dispersal vectors are well known (Schupp et al. 2010; Guiden et al. 2015). While there is evidence that many seed plants are adapted to endozoochorous dispersal (e.g., Herrera 2001), it is largely unknown whether this might also occur in other taxa, such as cryptogams.

Cryptogams include algae, lichens, bryophytes, and ferns, which have in common that they reproduce and disperse via spores instead of seeds. It is well established that the spores of cryptogams can be dispersed by wind, water, or exozoochory (Page 2002; Glime 2013). Recently, it has been shown that spores and even fragments of cryptogams, which have been consumed by gastropods, can survive the gut passage and regenerate from feces of gastropods, implying the potential for endozoochorous dispersal also in these taxa (Boch et al. 2011, 2013, 2015). However, whether spores can also survive the digestive tract of cryptogam-eating herbivores other than gastropods has never been tested in controlled feeding experiments.

Ferns are a very diverse taxonomic group inhabiting various terrestrial and some aquatic habitats. Globally, more humid regions harbor a higher fern species richness than drier ones (Kreft et al. 2010). Although many fern species produce toxic compounds (e.g., Carlisle and Ellis 1968; Smith 1997), various herbivores feed on them (Balick et al. 1978; Cooper-Driver 1990; Mesipuu et al. 2009; Sawamura et al. 2009; Arosa et al. 2010). In Europe, fern species occur in various habitats and can be characterized according to their ecological preferences (e.g., Landolt's ecological indicator values; Landolt et al. 2010). Furthermore, leaf-structural characteristics vary depending on the habitat, with overall tougher leaves in more sunny and dry habitats than in rather wet and shady ones (e.g., Tutin et al. 1993), which might affect herbivory. However, it is not known whether herbivores prefer fern species from particular habitats and whether spores of ferns from different habitats differently survive the gut passage of herbivores (Boch et al. 2013). Such preferences and differential survival have already been shown for seed plants (e.g., Türke et al. 2012) and might be applicable to endozoochorous dispersal in ferns as well.

Therefore, we fed leaves with mature sporangia of 13 fern species from different forest and open habitats indicated by different light indicator values to three polyphagous herbivore species and recorded the germination of fern spores from our experimental species after their passage through the guts of the herbivores. In particular, we addressed the following questions: (1) How common is it among fern spores to survive and germinate after being eaten by herbivores? (2) Does germination success of spores differ among fern species from different habitats? (3) Do herbivore species differ in their potential to endozoochorously disperse fern spores?

Materials and methods

Fern species

We chose 13 fern species that differ in their Landolt indicator values for light (Lv; Landolt et al. 2010). Landolt indicator values are estimates of the realized niche position of plants and range on an ordinal scale from 1 for shade-tolerant species often growing in forests to 5 for light-demanding species usually growing in open habitats. The selected species had light indicator values between 2 and 5 (Table 1).

Herbivore species

We chose three widespread herbivore species with a broad ecological amplitude to cover feeding on plants from different habitats: the slug *Arion vulgaris* (Moquin-Tandon) (Syn.: *A. lusitanicus* Mabille; Spanish slug; Arionidae) is a species of wide ecological amplitude and has an omnivorous feeding behavior. It is very common across Central Europe (Speiser 2001; Pfenninger et al. 2014). The cricket *Acheta domesticus* (L.) (house cricket; Gryllidae, Orthoptera) is native to Southwest Asia and escaped from cultivation (e.g., it is commonly used as food for other animals such as amphibians and reptiles) and is now distributed worldwide. The species mainly occurs in continuously warm and humid places (Baur et al. 2006). The caterpillar *Mamestra brassicae* (L.) (cabbage moth; Noctuidae, Lepidoptera) has a Palearctic distribution and is widespread in Europe. The species occurs in various forest and open habitats. Its larval stage is polyphagous and is known to feed on more than 70 plant species of more than 20 families (Rojas et al. 2000). Because of its polyphagy, the species is a perfect study organism frequently used in bioassays (e.g., Kempel et al. 2013).

Table 1 Experimental fern species with Landolt indicator values for light (Lv; Landolt et al. 2010)

Fern species	Family	Lv	Native distribution	Habitat	IPEN number Botanical Garden Bern
Phyllitis scolopendrium (L.) Newm.	Aspleniaceae	2	Northern hemisphere	Calcareous rocks in shady and humid sites	XX-0-BERN-2005/573GP
Athyrium filix-femina (L.) Roth	Woodsiaceae	2	Northern hemisphere	Mainly on moderately humid soils in various forests	CH-0-BERN-1973/114WS
Dryopteris filix-mas (L.) Schott	Dryopteridaceae	2	Northern hemisphere	Mainly on moderately humid soils in various forests	XX-0-BERN-1950/8301GP
Asplenium trichomanes L.	Aspleniaceae	3	Cosmopolitan	Various rocky habitats	XX-0-BERN-2005/503GP
Cystopteris fragilis (L.) Bernh.	Cystopteridaceae	3	Cosmopolitan	Various rocky habitats	XX-0-BERN-2005/627GP
Dryopteris oreades Adans.	Dryopteridaceae	3	Europe and Caucasus	Rocks and scree slopes in mountain areas	XX-0-BERN-1950/9910WP
Polypodium vulgare L.	Polypodiaceae	3	Northern hemisphere	On rocks and as epiphyte in forests and open habitats	XX-0-BERN-2005/628GP
Adiantum capillus-veneris L.	Pteridaceae	3	Cosmopolitan	Warm and humid temperate to tropical conditions	XX-0-BERN-2009/166GP
Asplenium ruta-muraria L.	Aspleniaceae	4	Northern hemisphere	Various rocks and walls in temperate conditions	XX-0-BERN-2005/658GP
Asplenium septentrionale (L.) Hoffm.	Aspleniaceae	4	Northern hemisphere	Crevices of acidic rocks	CH-0-BERN-2012/83WP
Asplenium ceterach L.	Aspleniaceae	5	Eurasia	Walls and rock fissures in Mediterranean regions	CH-0-BERN-1950/6124WP
Cyrtomium fortunei J. Sm.	Dryopteridaceae	5	Eastern Asia	Various humid-warm and open habitats	XX-0-BERN-2009/396GP
Pteris vittata L.	Pteridaceae	5	Paleotropics	Various dry limestone habitats	XX-0-BERN-2001/26GP

Information on native distribution and habitats of ferns are from Tutin et al. (1993) and Lauber et al. (2012). The International Plant Exchange Network (IPEN) numbers refer to the database entry of the living collection of the Botanical Garden of Bern where the fern leaves were collected

Collection of experimental species

In summer 2013, we collected several leaves with mature sporangia from each of the 13 fern species and 130 individuals of *Arion vulgaris* in the Botanical Garden of Bern (Switzerland; 46°57′N, 7°26′E). We further bought mature house crickets in a pet shop in Bern. We obtained *Mamestra brassicae* egg batches from the Entomology Laboratory of Wageningen University (Netherlands). After hatching, we grew the larvae on an artificial diet for two weeks in a climate chamber (25 °C; 12/12 h light/-dark cycle).

Feeding experiment and cultivation of ferns

We performed a factorial experiment feeding each of the 13 fern species to ten individuals of each of the three herbivore species (in total we used 130 individuals of each herbivore species). Before feeding the ferns, we kept the herbivores on an artificial diet for 24 h to avoid adaptation to specific plant species. Then, we randomly selected ten individuals of each herbivore species and transferred each slug into a fauna box (180 × 135 × 65 mm) and each caterpillar and cricket into a Petri dish (5 cm diameter for caterpillars and 10 cm diameter for crickets), where

we fed them with fern leaflets with mature sporangia and provided water using a water-sprayer.

Fauna boxes and Petri dishes were then placed in climate chamber with a 18/16 °C, 16/8 h day/night cycle (seven neon lights per 70 cm × 70 cm area: Philips 17 W, F17T8/TL741/ALTO, 4100 K, with each approx. 1325 lumens). After 48 h, we cleaned the herbivores under running water to avoid external contamination with spores and transferred them into new fauna boxes (slugs) or Petri dishes (crickets and caterpilars) for defecation. After 24 h, we collected all fecal pellets from each herbivore individual and transferred them into new Petri dishes of 5 cm diameter. With this procedure, we ensured that all fecal pellets tested for spore germination did not have any direct contact with plant material used during the feeding phase.

The Petri dishes with the fecal pellets contained the culture medium phytagel (Sigma Co., USA) without nutrients, to reduce bacterial and fungal growth, and were incubated in a climate cabinet for three months (15 °C; 16/8 h light/dark cycle; seven neon lights per 70 cm × 70 cm area with 50 cm distance between the plants and the lights: Philips 17 W, F17T8/TL741/ALTO, 4100 K, with each approx. 1325 lumens). Every other week, we randomized the position of the Petri dishes. We then inspected all the Petri dishes under a dissecting microscope and recorded whether any spores had germinated into fern prothallia from the feces in each Petri dish after 46 days and again after 81 days. A total of 23 herbivore individuals did not defecate at all, independent of fern or herbivore species (Chi-square test, p values >0.455) and are therefore treated as missing values.

Statistical analysis

We analyzed the germination of spores as a binomial variable with a generalized linear model (glm) and tested for differences among fern and herbivore species. We also included the Landolt indicator value for light and its interaction with fern and herbivore species. The Landolt indicator value for light was tested against the remaining variation among fern species using an F-test. Data were analyzed using R, v3.0.2 (R Development Core Team 2013).

Results

After 46 days, fern spores had germinated from feces of the herbivores in 66 % of the 367 samples (Fig. 1), indicating that fern spores can indeed survive the gut passage of herbivores. At this stage, the number of successfully germinating samples differed among the fern species, ranging from 52 % in *A. ceterach* to 86 % in *A. filix-femina*. However, the variation in germination among fern species could not be explained by the light indicator values of ferns, implying that ferns from different habitats are not differently adapted to endozoochorous dispersal (Table 2).

Spore germination was significantly higher from feces of *Arion vulgaris* (78 % of the 125 samples) and *Acheta domesticus* (70 % of the 118 samples) than from feces of *Mamestra brassicae* (50 % of the 124 samples; Fig. 2). As the interaction between fern and herbivore species was not significant, there was no indication that certain fern species germinated better after consumption by certain herbivores (Table 2).

After 81 days, fern spores had germinated from the herbivores feces in 85 % of the 367 samples (Fig. 1). At this stage, there were no longer any significant differences in spore germination success between different herbivore and fern species (Figs. 1, 2; Table 2). Germination success was higher than 76 % for all fern species and higher than 80 % for all herbivores. These data suggest that fern spores generally have a high chance to survive the gut passage of all used herbivore species and to develop into viable gametophytes.

Discussion

In our study, fern spores survived the gut passage of different invertebrate herbivores, germinated from feces and developed into gametophytes. Fern endozoochory by slugs had only recently been shown in a smaller set of three fern species (*Athyrium filix-femina, Dryopteris filix-mas, Gymnocarpium robertianum* (Hoffm.) Newman) and four bryophyte species, all from similar habitats (Boch et al. 2013). Similarly, fern growth has been observed from incubated feces of reindeer (Bråthen et al. 2007) and earthworms (van

Fig. 1 Differences in the germination success of spores among 13 fern species with different light indicator values (ordered from lowest to highest light indicator values) after 46 and 81 days (means + SEM). *Different letters* denote significant differences among least square means from our model at $p < 0.05$ (post hoc Tukey's test). *Lowercase letters* denote differences in germination success among fern species after 46 days, *capital letters* denote differences after 81 days
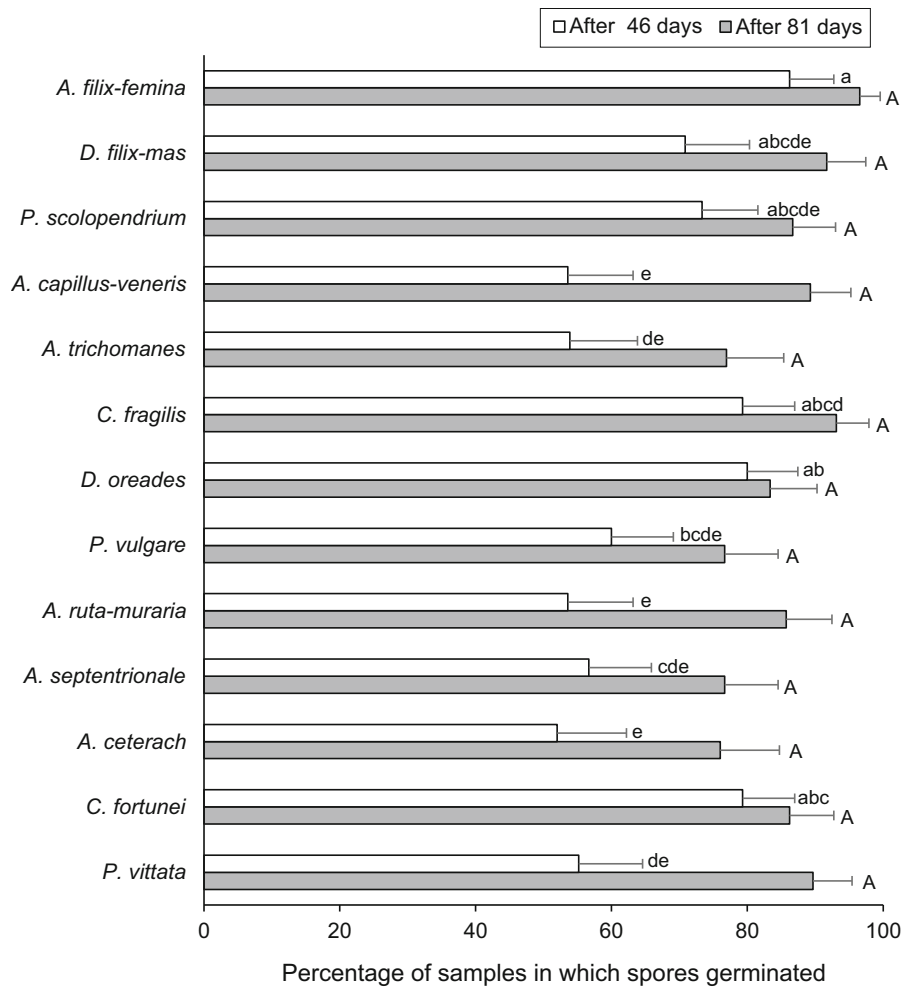

Table 2 GLM analysis testing for differences in the germination success of spores among 13 fern species with different light indicator values and among the three herbivore species after 46 and 81 days
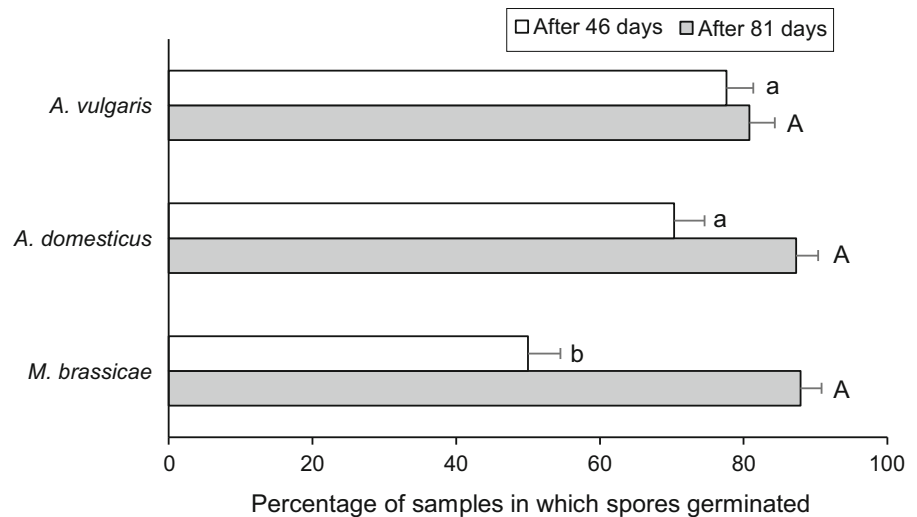
	df	Number of samples with germination success after 46 days		Number of samples with germination success after 81 days	
		Deviance changes/*F*-value	*p*	Deviance changes/*F*-value	*p*
Light value (Lv)	1	*2.47*	0.144	*1.49*	0.248
Fern species (Fs)	11	20.77	**0.036**	11.94	0.368
Herbivore species (Hs)	2	23.31	**<0.001**	3.22	0.200
Lv × Hs	2	*0.60*	0.555	*0.62*	0.550
Fs × Hs	22	27.33	0.199	15.12	0.615
Residuals	366	470.81		306.60	

Given are the deviance changes or the *F*-values (in italics). Significant differences are indicated by bold *p* values

Tooren and During 1988), although endozoochorous fern dispersal was not tested experimentally for these herbivores. Here, we show for a much larger set of species that all 13 fern species were eaten by all three herbivore species with no preferences for fern species from different habitats. Despite differences in spore germination among ferns in our first census (but not in the second), these differences were not related to

Fig. 2 The effect of herbivore species on the germination success of spores after 46 and 81 days (means + SEM). *Different letters denote significant differences among least square means from our model at* $p < 0.05$ *(post hoc Tukey's test). Lowercase letters denote differences in germination success among herbivore species after 46 days, capital letters denote differences in germination success among herbivore species after 81 days*

habitat preferences. However, germination time of spores is affected by temperature and every fern species seems to have an optimal germination temperature (e.g., Pangua et al. 1994; Qintanilla et al. 2008). This may possibly explain the differences in spore germination among our experimental fern species in our first census.

We observed considerable germination success and the potential to develop into fern prothallia for all of the fern species whose spores passed through the guts of all the herbivore species assessed in our study. These findings of generally high survival ability of spores through the gut passage of herbivores suggest there are likely no specific adaptations among fern species from particular habitats to endozoochorous dispersal. This leads us to suggest that endozoochorous dispersal of fern spores is a general phenomenon among fern-eating herbivores and questions the traditional view of an entirely antagonistic relationship between herbivores and ferns (e.g., Mesipuu et al. 2009; Sawamura et al. 2009). Nevertheless, it will remain interesting to test in further experiments, whether particular plant traits influence fern endozoochory (e.g., toxic compounds, spore anatomy).

The relative importance of endozoochory versus dispersal by water or wind in ferns remains unknown. Endozoochorous dispersal distances depend on the mobility and the gut passage speed of the herbivores

(Hickey et al. 1999). In our case, the traveled distances per day of the experimental herbivores are rather short (Crickets <30 m, Brouwers et al. (2011) for wood cricket which is closely related to the house cricket; slugs <15 m, Türke et al. (2010); caterpillars <1 m, Mauricio and Bowers (1990) for two Lepidopteran larvae). Thus, dispersal distances by small invertebrate herbivores via endozoochory are likely shorter than by wind, which may disperse spores over long distances. Nevertheless, endozoochory may affect the diversity of ferns at a local scale. In a common garden experiment, Boch et al. (2015) demonstrated that bryophyte-eating slugs can increase establishment, local population sizes, and species richness of bryophytes via endozoochory of spores. This indicates that even small animals can be important dispersers for plants reproducing by spores. Moreover, it is likely that feces are deposited in areas that are suitable for fern establishment and can promote growth as it is rich in nutrients. This may lead to higher establishment success after endozoochory than after wind dispersal. However, this is still conjectural and thus needs experimental tests comparing the germination rate and establishment success of wind-dispersed versus endozoochorously dispersed spores.

The differences in germination success among the three herbivore species after 46 days, with lower germination from feces of the caterpillar *Mamestra*

brassicae than of the other herbivore species, disappeared after 81 days. This might be explained by the more compact and dryer feces of *M. brassicae* compared with the other herbivores. Possibly, the feces of *M. brassicae* needed longer to soak humidity from the culture medium or it was harder for young gametophytes to penetrate the surface of the feces than of the ones of the other herbivores. In any case, the disappearance of statistical differences from the first to the second census underlined the importance of enough germination time, especially in experiments involving many species.

Conclusions

The overall high germination rate of spores among all fern species from different habitats together with the consistency across three tested herbivores and the few observational studies on other animals strongly imply that endozoochorous dispersal of fern spores is a general and taxonomically widespread phenomenon among fern-eating herbivores. Thus, given that fern herbivory is common in nature, fern endozoochory might occur more frequently than expected and it may well be that all fern-eating herbivores can act as potential dispersal vectors.

References

Arosa ML, Ramos JA, Quintanilla D, Brown LG (2010) First report of fern (*Culcita macrocarpa*) spore consumption by a small mammal (*Apodemus sylvaticus*). Mamm Biol 75:115–121

Balick MJ, Furth DG, Cooper-Driver G (1978) Biochemical and evolutionary aspects of arthropod predation on ferns. Oecologia 35:55–89

Baur B, Baur H, Roesti C, Roesti D (2006) Die Heuschrecken der Schweiz. Haupt Verlag, Bern, p 352

Boch S, Prati D, Werth S, Rüetschi J, Fischer M (2011) Lichen endozoochory by snails. PLoS One 6(4):e18770

Boch S, Berlinger M, Fischer M, Knop E, Nentwig W, Türke M, Prati D (2013) Fern and bryophyte endozoochory by slugs. Oecologia 172:817–822

Boch S, Fischer M, Knop E, Allan E (2015) Endozoochory by slugs can increase bryophyte establishment and species richness. Oikos 124:331–336

Bråthen KA, González VT, Iversen M, Killengreen S, Ravolainen VT, Ims RA, Yoccoz NG (2007) Endozoochory varies with ecological scale and context. Ecography 30:308–320

Brouwers NC, Newton AC, Bailey S (2011) The dispersal ability of wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae) in a wooded landscape. Eur J Entomol 108:117–125

Carlisle DB, Ellis PE (1968) Bracken and locust ecdysones: their effects on molting in the desert locust. Science 159:1472–1474

Cooper-Driver GA (1990) Defense strategies in bracken, *Pteridium aquilinum* (L.) Kuhn. Ann Mo Bot Gard 77:281–286

Cousens R, Dytham C, Law R (2008) Dispersal in plants: a population perspective. Oxford University Press, Oxford, p 221

Crawley MJ (1983) Herbivory: the dynamics of animal-plant ineractions. Blackwell Scientific Publications, Oxford, p 437

Development Core Team R (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Glime JM (2013) Invertebrates. Chapter 4. In: Glime JM (ed) Bryophyte Ecology. Volume 2. Bryological Interaction. [online]. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. http://www.bryoecol.mtu.edu/. Accessed 19 Nov 2015

Guiden P, Gorchov DL, Nielsen C, Schauber E (2015) Seed dispersal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), by white-tailed deer in a fragmented agricultural-forest matrix. Plant Ecol 216:939–950

Herrera CM (2001) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds) Plant–animal interactions: an evolutionary approach. Blackwell Science, Oxford, pp 185–208

Hickey JR, Flynn RW, Buskirk SW, Gerow KG, Wilson MF (1999) An evaluation of a mammalian predator, *Martes americana*, as a disperser of seeds. Oikos 87:499–508

Kempel A, Nater P, Fischer M, van Kleunen M (2013) Plant-microbe-herbivore interactions in invasive and non-invasive alien plant species. Funct Ecol 27:498–508

Kreft H, Jetz W, Mutke J, Barthlott W (2010) Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. Ecography 33:408–419

Landolt E, Bäumler B, Erhardt A et al (2010) Flora Indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. 2nd edn. Haupt Verlag, Bern, p 378

Lauber K, Wagner G, Gygax A (2012) Flora Helvetica, 5th edn. Haupt Verlag, Bern, p 1656

Lind EM, Borer E, Seabloom E et al (2013) Life-history constraints in grassland plant species: a growth–defence trade-off is the norm. Ecol Lett 16:513–521

Mauricio R, Bowers D (1990) Do caterpillars disperse their damage?: larval foraging behavior of two herbivores, *Euphydryas phaeton* (Nymphalidae) and *Pieris rapae* (Pieridae). Ecol Entomol 15:153–161

Mesipuu M, Shefferson RP, Kull T (2009) Weather and herbivores influence fertility in the endangered fern *Botrychium multifidum* (S.G. Gmel.) Rupr. Plant Ecol 203:23–31

Page CN (2002) Ecological strategies in fern evolution: a neopteridological overview. Rev Palaeobot Palyno 119:1–33

Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. Am Nat 129:407–416

Pangua E, Lindsay S, Dyer A (1994) Spore germination and gamtophyte development in three species of *Asplenium*. Ann Bot 73:587–593

Pfenninger M, Weigand A, Bálint M, Klussmann-Kolb A (2014) Misperceived invasion: the Lusitanian slug (*Arion lusitanicus* auct. non-Mabille or *Arion vulgaris* Moquin-Tandon 1855) is native to Central Europe. Evol Appl 7:702–713

Qintanilla LG, Pajarón S, Pangua E, Amigo J (2008) Effect of temperature on germination in northernmost populations of *Culcita macrocarpa* and *Woodwardia radicans*. Plant Biol 2:612–617

Rojas JC, Wyatt TD, Birch MC (2000) Flight and oviposition behavior toward different host plant species by the cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera. Noctuidae). J Insect Behav 13:247–254

Sawamura M, Kawakita A, Kato M (2009) Fern-spore-feeder interaction in temperate forests in Japan: sporing phenology and spore-feeding insect community. Am J Bot 96:594–604

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytol 188:333–353

Smith BL (1997) The toxicity of bracken fern (genus *Pteridium*) to animals and its relevance to man. In: D'Mello JPF (ed) Handbook of plant and fungal toxicants. CRC Press, Boca Raton, pp 63–76

Speiser B (2001) Food and feeding behaviour. In: Barker GM (ed) The biology of terrestrial mollusks. CABI, Wallingford, pp 259–288

Traveset A, Rodríguez-Pérez J, Pías B (2008) Seed trait changes in dispersers' guts and consequences for germination and seedling growth. Ecology 89:95–106

Türke M, Heinze E, Andreas K et al (2010) Seed consumption and dispersal in ant-dispersed plants by slugs. Oecologia 163:681–693

Türke M, Andreas K, Gossner MM et al (2012) Are gastropods, rather than ants, important dispersers of seeds of myrmecochorous forest herbs? Am Nat 179:124–131

Tutin TG, Burges NA, Chater AO et al (1993) Flora Europaea, Psilotaceae to platanaceae. Vol 1. Cambridge University Press, Cambridge, p 581

van Tooren BF, During HJ (1988) Viable plant diaspores in the guts of earthworms. Acta Bot Neerl 37:181–185

Walling LL (2000) The myriad plant responses to herbivores. J Plant Growth Regul 19:195–216