

Oikos

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Heger, T. and Jeschke, J. M. 2014. The enemy release hypothesis as a hierarchy of hypotheses. –
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Appendix 1–4

Heger, T. and Jeschke, J. M. 2014. The enemy release hypothesis as a hierarchy of hypotheses. – *Oikos* 123: 741–750.

Supplementary material Appendix 1

Studies included in the analysis, together with their level of empirical support for each sub-hypothesis of the enemy release hypothesis (supporting, undecided, or questioning).

1. Sub-hypothesis "Less damage by enemies"
 - 1.1. Comparison of aliens versus natives
 - 1.1.1. No differentiation of enemy type

Supported

Carpenter, D. and Cappuccino, N. 2005. Herbivory, time since introduction and the invasiveness of exotic plants. - *J. Ecol.* 93: 315-321.

Cincotta, C. L. et al. 2009. Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). - *Biol. Invasions* 11: 379-388.

Dietz, H. et al. 2004. Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahe, Seychelles. - *Biol. Invasions* 6: 511-521.

Gollan, J. R. and Wright, J. T. 2006. Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. - *Mar. Freshw. Res.* 57: 685-694.

Han, X. M. et al. 2008. Comparison of damage to native and exotic tallgrass prairie plants by natural enemies. - *Plant Ecol.* 198: 197-210.

Hill, S. B. and Kotanen, P. M. 2010. Phylogenetically structured damage to Asteraceae: susceptibility of native and exotic species to foliar herbivores. - *Biol. Invasions* 12: 3333-3342.

Liu, H. et al. 2007. Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. - *Biol. Invasions* 9: 773-781.

Lombardero, M. J. et al. 2008. Role of plant enemies in the forestry of indigenous vs. nonindigenous pines. - *Ecol. Appl.* 18: 1171-1181.

Matter, S. F. et al. 2012. Invading from the garden? A comparison of leaf herbivory for exotic and native plants in natural and ornamental settings. - *Insect Sci.* 19: 677-682.

Schutzenhofer, M. R. et al. 2009. Herbivory and population dynamics of invasive and native *Lespedeza*. - *Oecologia* 161: 57-66.

Siemann, E. and Rogers, W. E. 2003. Herbivory, disease, recruitment limitation, and success of alien and native tree species. - *Ecology* 84: 1489-1505.

Siemann, E. and Rogers, W. E. 2006. Recruitment limitation, seedling performance and persistence of exotic tree monocultures. - *Biol. Invasions* 8: 979-991.

Sugiura, S. 2010. Associations of leaf miners and leaf galls with island plants of different residency histories. - *Journal of Biogeography* 37: 237-244.

White, E. M. et al. 2008. Test of the enemy release hypothesis: The native magpie moth prefers a native fireweed (*Senecio pinnatifolius*) to its introduced congener (*S. madagascariensis*). - *Austral. Ecol.* 33: 110-116.

Zheng, Y. L. et al. 2012. Invasive *Eupatorium adenophorum* suffers lower enemy impact on carbon assimilation than native congeners. - *Ecol. Res.* 27: 867-872.

Undecided

Agrawal, A. A. et al. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. - *Ecology* 86: 2979-2989.

Funk, J. L. and Throop, H. L. 2010. Enemy release and plant invasion: patterns of defensive traits and leaf damage in Hawaii. - *Oecologia* 162: 815-823.

Hill, S. B. and Kotanen, P. M. 2011. Phylogenetic structure predicts capitular damage to Asteraceae better than origin or phylogenetic distance to natives. - *Oecologia* 166: 843-851.

Leger, E. A. et al. 2007. The interaction between soil nutrients and leaf loss during early 14 establishment in plant invasion. - *For. Sci.* 53: 701-709.

Norghauer, J. M. et al. 2011. Island invasion by a threatened tree species: evidence for natural enemy release of mahogany (*Swietenia macrophylla*) on Dominica, Lesser Antilles. - *PloS one* 6: e18790-e18790.

Parker, I. M. and Gilbert, G. S. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. - *Ecology* 88: 1210-1224.

Vasquez, E. C. and Meyer, G. A. 2011. Relationships among leaf damage, natural enemy release, and abundance in exotic and native prairie plants. - *Biol. Invasions* 13: 621-633.

Questioned

Agrawal, A. A. and Kotanen, P. M. 2003. Herbivores and the success of exotic plants: a phylogenetically controlled experiment. - *Ecol. Lett.* 6: 712-715.

- Ashton, I. W. and Lerdau, M. T. 2008. Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. - *Divers. Distrib.* 14: 169-178.
- Ferreras, A. E. and Galetto, L. 2010. From seed production to seedling establishment: Important steps in an invasive process. - *Acta Oecologica - International Journal of Ecology* 36: 211 - 218.
- Hartley, M. K. et al. 2010. Comparisons of arthropod assemblages on invasive and native trees: abundance, diversity and damage. - *Arthropod-Plant Interactions* 4: 237-245.
- Heard, M. J. and Sax, D. F. 2012. Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. - *Ecol. Lett.* 16: 206-213.
- Morrison, J. A. and Mauck, K. 2007. Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. - *J. Ecol.* 95: 1036-1049.
- Munoz, M. C. and Ackerman, J. D. 2011. Spatial distribution and performance of native and invasive *Ardisia* (Myrsinaceae) species in Puerto Rico: the anatomy of an invasion. - *Biol. Invasions* 13: 1543-1558.
- Pirk, G. I. and Farji-Brener, A. G. 2012. Foliar herbivory and its effects on plant growth in native and exotic species in the Patagonian steppe. - *Ecol. Res.* 27: 903-912.
- Radho-Toly, S. et al. 2001. Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. - *Aust. J. Ecol.* 26: 500-506.
- Stricker, K. B. and Stiling, P. 2012. Herbivory by an introduced Asian weevil negatively affects population growth of an invasive Brazilian shrub in Florida. - *Ecology* 93: 1902-1911.
- Sullivan, J. J. et al. 2008. Novel host associations and habitats for *Senecio*-specialist herbivorous insects in Auckland. - *N. Z. J. Ecol.* 32: 219-224.
- Suwa, T. and Louda, S. M. 2012. Combined effects of plant competition and insect herbivory hinder invasiveness of an introduced thistle. - *Oecologia* 169: 467-476.

1.1.2. Generalists

Questioned

- Strauss, S. Y. et al. 2009. Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. - *Ecology* 90: 419-429.

1.1.3. Specialists

Supported

Hartley, M. K. et al. 2010. Comparisons of arthropod assemblages on invasive and native trees: abundance, diversity and damage. - *Arthropod-Plant Interactions* 4: 237-245.

Liu, H. et al. 2007. Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. - *Biol. Invasions* 9: 773-781.

1.2. Comparison of aliens in native versus in invaded range

1.2.1. No differentiation of enemy type

Supported

Adams, J. M. et al. 2009. A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. - *Biol. Invasions* 11: 1005-1016.

Alba, C. and Hufbauer, R. 2012. Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. - *Biol. Invasions* 14: 2505-2518.

Cripps, M. G. et al. 2010. Enemy release does not increase performance of *Cirsium arvense* in New Zealand. - *Plant Ecol.* 209: 123-134.

Ebeling, S. K. et al. 2008. The invasive shrub *Buddleja davidii* performs better in its introduced range. - *Divers. Distrib.* 14: 225-233.

Genton, B. J. et al. 2005. Enemy release but no evolutionary loss of defence in a plant invasion: an inter-continental reciprocal transplant experiment. - *Oecologia* 146: 404-414.

Lewis, K. C. et al. 2006. Geographic patterns of herbivory and resource allocation to defense, growth, and reproduction in an invasive biennial, *Alliaria petiolata*. - *Oecologia* 148: 384-395.

Shwartz, A. et al. 2009. The effect of enemy-release and climate conditions on invasive birds: a regional test using the rose-ringed parakeet (*Psittacula krameri*) as a case study. - *Divers. Distrib.* 15: 310-318.

Vila, M. et al. 2005. Evidence for the enemy release hypothesis in *Hypericum perforatum*. - *Oecologia* 142: 474-479.

Wolfe, L. M. 2002. Why Alien Invaders Succeed: Support for the Escape-from-Enemy Hypothesis. - *Am. Nat.* 160: 705-711.

Undecided

DeWalt, S. J. et al. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. - Ecology 85: 471-483.

Hinz, H. L. et al. 2012. Biogeographical comparison of the invasive *Lepidium draba* in its native, expanded and introduced ranges. - Biol. Invasions 14: 1999-2016.

Questioned

Roy, B. A. et al. 2011. Population regulation by enemies of the grass *Brachypodium sylvaticum*: demography in native and invaded ranges. - Ecology 92: 665-675.

Torchin, M. E. et al. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. - Biol. Invasions 3: 333-345.

Williams, J. L. et al. 2010. Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. - Ecology 91: 1355-1366.

1.2.2. Generalists

No empirical tests available

1.2.3. Specialists

No empirical tests available

1.3. Comparison of invasive versus non-invasive aliens

1.3.1. No differentiation of enemy type

Supported

Cappuccino, N. and Carpenter, D. 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. - Biology Letters 1: 435-438.

Jogesh, T. et al. 2008. Herbivory on invasive exotic plants and their non-invasive relatives. - Biol. Invasions 10: 797-804.

Undecided

Vasquez, E. C. and Meyer, G. A. 2011. Relationships among leaf damage, natural enemy release, and abundance in exotic and native prairie plants. - Biol. Invasions 13: 621-633.

Questioned

Liu, H. et al. 2007. Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. - *Biol. Invasions* 9: 773-781.

Matter, S. F. et al. 2012. Invading from the garden? A comparison of leaf herbivory for exotic and native plants in natural and ornamental settings. - *Insect Sci.* 19: 677-682.

Parker, I. M. and Gilbert, G. S. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. - *Ecology* 88: 1210-1224.

1.3.2. Generalists

Supported

Jogesh, T. et al. 2008. Herbivory on invasive exotic plants and their non-invasive relatives. - *Biol. Invasions* 10: 797-804.

1.3.3. Specialists

Questioned

Liu, H. et al. 2007. Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. - *Biol. Invasions* 9: 773-781.

2. Sub-hypothesis "Less infestation with enemies"

2.1. Comparison of aliens versus natives

2.1.1. No differentiation of enemy type

Supported

Blakeslee, A. M. H. et al. 2012. Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges. - *J. Biogeogr.* 39: 609-622.

Cameron, G. N. and Spencer, S. R. 2010. Entomofauna of the introduced Chinese Tallow Tree. - *Southwest. Nat.* 55: 179-192.

- Cincotta, C. L. et al. 2009. Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). - Biol. Invasions 11: 379-388.
- Engelkes, T. et al. 2012. Contrasting patterns of herbivore and predator pressure on invasive and native plants. - Basic Appl. Ecol. 13: 725-734.
- Gendron, A. D. et al. 2012. Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. - Biol. Invasions 14: 367-384.
- Genner, M. J. et al. 2008. Resistance of an invasive gastropod to an indigenous trematode parasite in Lake Malawi. - Biol. Invasions 10: 41-49.
- Gollan, J. R. and Wright, J. T. 2006. Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. - Mar. Freshw. Res. 57: 685-694.
- Hartley, M. K. et al. 2010. Comparisons of arthropod assemblages on invasive and native trees: abundance, diversity and damage. - Arthropod-Plant Interactions 4: 237-245.
- Hawkes, C. V. et al. 2010. Origin, local experience, and the impact of biotic interactions on native and introduced *Senecio* species. - Biol. Invasions 12: 113-124.
- Krakau, M. et al. 2006. Native parasites adopt introduced bivalves of the North Sea. - Biol. Invasions 8: 919-925.
- Kvach, Y. and Stepien, C. A. 2008. Metazoan parasites of introduced round and tubenose gobies in the Great Lakes: Support for the "Enemy Release Hypothesis". - J. Gt. Lakes Res. 34: 23-35.
- Lima, M. R. et al. 2010. Low prevalence of haemosporidian parasites in the introduced house sparrow (*Passer domesticus*) in Brazil. - Acta Parasitol. 55: 297-303.
- Miller, A. et al. 2008. Use of the introduced bivalve, *Musculista senhousia*, by generalist parasites of native New Zealand bivalves. - N. Z. J. Mar. Freshw. Res. 42: 143-151.
- Proches, S. et al. 2008. Herbivores, but not other insects, are scarce on alien plants. - Austral. Ecol. 33: 691-700.
- Roche, D. G. et al. 2010. Higher parasite richness, abundance and impact in native versus introduced cichlid fishes. - Int. J. Parasitol. 40: 1525-1530.
- Siemann, E. and Rogers, W. E. 2006. Recruitment limitation, seedling performance and persistence of exotic tree monocultures. - Biol. Invasions 8: 979-991.
- White, E. M. et al. 2008. Diversity and abundance of arthropod floral visitor and herbivore assemblages on exotic and native *Senecio* species. - Plant Prot. Q. 23.

Wikstrom, S. A. et al. 2006. Increased chemical resistance explains low herbivore colonization of introduced seaweed. - *Oecologia* 148: 593-601.

Undecided

Agrawal, A. A. et al. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. - *Ecology* 86: 2979-2989.

Dang, C. et al. 2009. Testing the enemy release hypothesis: trematode parasites in the non-indigenous Manila clam *Ruditapes philippinarum*. - *Hydrobiologia* 630: 139-148.

Knevel, I. C. et al. 2004. Release from native root herbivores and biotic resistance by soil pathogens in a new habitat both affect the alien *Ammophila arenaria* in South Africa. - *Oecologia* 141: 502-510.

Lacerda, A. C. F. et al. 2013. Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects. - *Parasitol. Res.* 112: 279-88.

Zuefle, M. E. et al. 2008. Effects of non-native plants on the native insect community of Delaware. - *Biol. Invasions* 10: 1159-1169.

Questioned

Ando, Y. et al. 2010. Community structure of insect herbivores on introduced and native *Solidago* plants in Japan. - *Entomol. Exp. Appl.* 136: 174-183.

Bassett, I. E. et al. 2012. Invertebrate community composition differs between invasive herb alligator weed and native sedges. - *Acta Oecol.* 41: 65-73.

Frenzel, M. and Brandl, R. 2003. Diversity and abundance patterns of phytophagous insect communities on alien and native host plants in the Brassicaceae. - *Ecography* 26: 723-730.

Kulfan, J. et al. 2010. Caterpillar assemblages on introduced blue spruce. differences from native Norway spruce. - *Allgemeine Forst- und Jagdzeitung* 181: 188-194.

Liu, H. et al. 2006. Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: Implications for the enemy release hypothesis. - *Fla. Entomol.* 89: 475-484.

Lombardero, M. J. et al. 2008. Role of plant enemies in the forestry of indigenous vs. nonindigenous pines. - *Ecol. Appl.* 18: 1171-1181.

Parker, I. M. and Gilbert, G. S. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. - *Ecology* 88: 1210-1224.

Pirk, G. I. and Farji-Brener, A. G. 2012. Foliar herbivory and its effects on plant growth in native and exotic species in the Patagonian steppe. - *Ecol. Res.* 27: 903-912.

2.1.2. Generalists

Questioned

Bassett, I. E. et al. 2012. Invertebrate community composition differs between invasive herb alligator weed and native sedges. - *Acta Oecol.* 41: 65-73.

Zuefle, M. E. et al. 2008. Effects of non-native plants on the native insect community of Delaware. - *Biol. Invasions* 10: 1159-1169.

2.1.3. Specialists

Supported

Liu, H. et al. 2006. Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: Implications for the enemy release hypothesis. - *Fla. Entomol.* 89: 475-484.

Questioned

Bassett, I. E. et al. 2012. Invertebrate community composition differs between invasive herb alligator weed and native sedges. - *Acta Oecol.* 41: 65-73.

Sullivan, J. J. et al. 2008. Novel host associations and habitats for *Senecio*-specialist herbivorous insects in Auckland. - *N. Z. J. Ecol.* 32: 219-224.

Zuefle, M. E. et al. 2008. Effects of non-native plants on the native insect community of Delaware. - *Biol. Invasions* 10: 1159-1169.

2.2. Comparison of aliens in native versus in invaded range

2.2.1. No differentiation of enemy type

Supported

Beckstead, J. and Parker, I. M. 2003. Invasiveness of *Ammophila arenaria*: Release from soil-borne pathogens? - *Ecology* 84: 2824-2831.

Blakeslee, A. M. H. et al. 2012. Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges. - *J. Biogeogr.* 39: 609-622.

Fenner, M. and Lee, W. G. 2001. Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. - *N. Z. J. Ecol.* 25: 95-99.

- Kvach, Y. and Stepien, C. A. 2008. Metazoan parasites of introduced round and tubenose gobies in the Great Lakes: Support for the "Enemy Release Hypothesis". - J. Gt. Lakes Res. 34: 23-35.
- Marzal, A. et al. 2011. Diversity, loss, and gain of malaria parasites in a globally invasive bird. - PloS one 6: e21905-e21905.
- Memmott, J. et al. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. - Acta Oecologica - International Journal of Ecology 21: 213-222.
- Mitchell, C. E. and Power, A. G. 2003. Release of invasive plants from fungal and viral pathogens. - Nature 421: 625-627.
- Prati, D. and Bossdorf, O. 2004. A comparison of native and introduced populations of the South African Ragwort *Senecio inaequidens* DC. in the field. - In: Breckle, S. W., Schweizer, B. and Fangmeier, A. (eds.), Results of worldwide ecological studies. Verlag Günter Heimbach, pp. 353-359.
- Reinhart, K. O. et al. 2010. Virulence of soil-borne pathogens and invasion by *Prunus serotina*. - New Phytol. 186: 484-495.
- Torchin, M. E. et al. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. - Biol. Invasions 3: 333-345.
- van Kleunen, M. and Fischer, M. 2009. Release from foliar and floral fungal pathogen species does not explain the geographic spread of naturalized North American plants in Europe. - J. Ecol. 97: 385-392.
- Vignon, M. et al. 2009. Host introduction and parasites: a case study on the parasite community of the peacock grouper *Cephalopholis argus* (Serranidae) in the Hawaiian Islands. - Parasitol. Res. 104: 775-782.
- Wikstrom, S. A. et al. 2006. Increased chemical resistance explains low herbivore colonization of introduced seaweed. - Oecologia 148: 593-601.

Undecided

- Alba, C. and Hufbauer, R. 2012. Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. - Biol. Invasions 14: 2505-2518.
- Ishtiaq, F. et al. 2006. Prevalence and evolutionary relationships of haematozoan parasites in native versus introduced populations of common myna *Acridotheres tristis*. - Proceedings of the Royal Society B-Biological Sciences 273: 587-594.

Marr, S. R. et al. 2008. Parasite loss and introduced species: a comparison of the parasites of the Puerto Rican tree frog, *Eleutherodactylus coqui*, in its native and introduced ranges. - Biol. Invasions 10: 1289-1298.

Questioned

Colautti, R. I. et al. 2005. Realized vs apparent reduction in enemies of the European starling. - Biol. Invasions 7: 723-732.

Cripps, M. G. et al. 2006. Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges. - J. Biogeogr. 33: 2107-2119.

Lacerda, A. C. F. et al. 2013. Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects. - Parasitol. Res. 112: 279-88.

Slothouber Galbreath, J. G. M. et al. 2010. Reduction in post-invasion genetic diversity in *Crangonyx pseudogracilis* (Amphipoda: Crustacea): a genetic bottleneck or the work of hitchhiking vertically transmitted microparasites? - Biol. Invasions 12: 191-209.

van der Putten, W. H. et al. 2005. Invasive plants and their escape from root herbivory: a worldwide comparison of the root-feeding nematode communities of the dune grass *Ammophila arenaria* in natural and introduced ranges. - Biol. Invasions 7: 733-746.

2.2.2. Generalists

Questioned

Cripps, M. G. et al. 2006. Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges. - J. Biogeogr. 33: 2107-2119.

Memmott, J. et al. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. - Acta Oecologica - International Journal of Ecology 21: 213-222.

2.2.3. Specialists

Supported

Cripps, M. G. et al. 2006. Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges. - J. Biogeogr. 33: 2107-2119.

Hansen, S. O. et al. 2006. Phytophagous insects of giant hogweed *Heracleum mantegazzianum* (Apiaceae) in invaded areas of Europe and in its native area of the Caucasus. - Eur. J. Entomol. 103: 387-395.

Hinz, H. L. et al. 2012. Biogeographical comparison of the invasive *Lepidium draba* in its native, expanded and introduced ranges. - Biol. Invasions 14: 1999-2016.

Imura, O. 2003. Herbivorous arthropod community of an alien weed *Solanum carolinense* L. . - Appl. Entomol. Zool. 38: 293-300.

Memmott, J. et al. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. - Acta Oecologica - International Journal of Ecology 21: 213-222.

Undecided

van der Putten, W. H. et al. 2007. Soil feedback of exotic savanna grass relates to pathogen absence and mycorrhizal selectivity. - Ecology 88: 978-988.

2.3. Comparison of invasive versus non-invasive aliens

2.3.1. No differentiation of enemy type

Questioned

Liu, H. et al. 2006. Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: Implications for the enemy release hypothesis. - Fla. Entomol. 89: 475-484.

Parker, I. M. and Gilbert, G. S. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. - Ecology 88: 1210-1224.

2.3.2. Generalists

No empirical tests available

2.3.3. Specialists

Questioned

Liu, H. et al. 2006. Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: Implications for the enemy release hypothesis. - Fla. Entomol. 89: 475-484.

3. Sub-hypothesis "Enhanced performance of alien species"

3.1. Comparison of aliens versus natives

3.1.1. No differentiation of enemy type

Supported

Roche, D. G. et al. 2010. Higher parasite richness, abundance and impact in native versus introduced cichlid fishes. - *Int. J. Parasitol.* 40: 1525-1530.

van der Putten, W. H. et al. 2007. Soil feedback of exotic savanna grass relates to pathogen absence and mycorrhizal selectivity. - *Ecology* 88: 978-988.

Undecided

Hawkes, C. V. et al. 2010. Origin, local experience, and the impact of biotic interactions on native and introduced *Senecio* species. - *Biol. Invasions* 12: 113-124.

Leger, E. A. et al. 2007. The interaction between soil nutrients and leaf loss during early 14 establishment in plant invasion. - *For. Sci.* 53: 701-709.

Schutzenhofer, M. R. et al. 2009. Herbivory and population dynamics of invasive and native *Lespedeza*. - *Oecologia* 161: 57-66.

Questioned

Blaney, C. S. and Kotanen, P. M. 2001. Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. - *J. Appl. Ecol.* 38: 1104-1113.

Blaney, C. S. and Kotanen, P. M. 2001. Post-dispersal losses to seed predators: an experimental comparison of native and exotic old field plants. - *Can. J. Bot.* 79: 284-292.

Dostal, P. 2010. Post-dispersal seed mortality of exotic and native species: Effects of fungal pathogens and seed predators. - *Basic Appl. Ecol.* 11: 676-684.

Grey, E. K. 2010. Effects of large enemies on success of exotic species in marine fouling communities of Washington, USA. - *Mar. Ecol. Prog. Ser.* 411: 89-U136.

Heard, M. J. and Sax, D. F. 2012. Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. - *Ecol. Lett.* 16: 206-213.

Lombardero, M. J. et al. 2008. Role of plant enemies in the forestry of indigenous vs. nonindigenous pines. - *Ecol. Appl.* 18: 1171-1181.

Miller, A. et al. 2008. Use of the introduced bivalve, *Musculista senhousia*, by generalist parasites of native New Zealand bivalves. - *N. Z. J. Mar. Freshw. Res.* 42: 143-151.

Morrison, J. A. and Mauck, K. 2007. Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. - *J. Ecol.* 95: 1036-1049.

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3.1.2. Generalists

Supported

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Undecided

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Questioned

Strauss, S. Y. et al. 2009. Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. - *Ecology* 90: 419-429.

3.1.3. Specialists

No empirical tests available

3.2. Comparison of aliens in native versus in invaded range

3.2.1. No differentiation of enemy type

Supported

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Undecided

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Questioned

Cripps, M. G. et al. 2010. Enemy release does not increase performance of *Cirsium arvense* in New Zealand. - Plant Ecol. 209: 123-134.

te Beest, M. et al. 2009. Plant-soil feedback induces shifts in biomass allocation in the invasive plant *Chromolaena odorata*. - J. Ecol. 97: 1281-1290.

3.2.2. Generalists

No empirical tests available

3.2.3. Specialists

No empirical tests available

3.3. Comparison of invasive versus non-invasive aliens

3.3.1. No differentiation of enemy type

Questioned

Andonian, K. et al. 2011. Range-expanding populations of a globally introduced weed experience negative plant-soil feedbacks. - PloS one 6: e20117-e20117.

3.3.2. Generalists

Questioned

Pearson, D. E. et al. 2011. Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. - Ecology 92: 1748-1757.

3.3.3. Specialists

No empirical tests available

3.4. Comparison of aliens with versus without enemies

3.4.1. No differentiation of enemy type

Supported

Reinhart, K. O. et al. 2010. Virulence of soil-borne pathogens and invasion by *Prunus serotina*. - *New Phytol.* 186: 484-495.

Undecided

Volin, J. C. et al. 2010. Does release from natural belowground enemies help explain the invasiveness of *Lygodium microphyllum*? A cross-continental comparison. - *Plant Ecol.* 208: 223-234.

Questioned

Ashton, I. W. and Ler dau, M. T. 2008. Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. - *Divers. Distrib.* 14: 169-178.

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3.4.2. Generalists

Supported

Eschtruth, A. K. and Battles, J. J. 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. - *Conserv. Biol.* 23: 388-399.

3.4.3. Specialists

No empirical tests available

Heger, T. and Jeschke, J. M. 2014. The enemy release hypothesis as a hierarchy of hypotheses. – *Oikos* 123: 741–750.

Supplementary material Appendix 2

Table A1. Unweighted evidence from empirical tests supporting, questioning, or being undecided about the enemy release hypothesis in its broadest formulation ('Total') and each of its sub-hypotheses. Chi-Square tests indicate whether the distribution of the three categories (supporting, undecided, or questioning) significantly deviates from an equal distribution. If yes (i.e. if $p < 0.05$, given in bold letters), we performed post-hoc binomial tests to compare the proportion of supporting vs. questioning studies for this (sub-)hypothesis (again, significant results ($p < 0.05$) are in bold letters).

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Total	176	44.3%	16.5%	39.2%	<0.001	0.510
Damage	59	49.2%	17.0%	33.9%	0.01	0.253
Infestation	69	53.6%	13.0%	33.3%	<0.001	0.092
Performance	48	25.0%	20.8%	54.2%	0.009	0.034
Aliens / natives	98	39.8%	17.4%	42.9%	0.003	0.824
Native / invaded range	56	60.7%	17.7%	21.4%	<0.001	0.002
Invasive / non-invasive	13	23.1%	7.7%	69.2%	0.018	0.146
Only aliens	9	22.2%	11.1%	66.7%	0.097	-
Generalists	12	25.0%	16.7%	58.3%	0.174	-
Specialists	14	57.1%	7.1%	35.7%	0.071	-
No differentiation	150	44.7%	17.3%	38.0%	<0.001	0.419

Table A2. Unweighted evidence from empirical tests supporting, questioning, or being undecided about the enemy release hypothesis, differentiated according to habitat type, taxonomic group, and research method. Results of statistical tests are given as in Table 1.

	n	Supported	Undecided	Questioned	χ^2	Binomial test
Terrestrial	147	40.8%	18.4%	40.8%	0.001	0.927
Freshwater	14	42.9%	7.1%	50.0%	0.109	-
Marine	15	20.0%	6.7%	73.3%	0.004	0.057
Plants	143	43.4%	17.5%	39.2%	<0.001	0.645
Algae	5	0.0%	0.0%	100.0%	0.007	0.063
Invertebrates	12	41.7%	8.3%	50.0%	0.174	-
Vertebrates	16	12.5%	18.8%	68.8%	0.010	0.022
Experimental	64	50.0%	23.4%	26.6%	0.017	0.044
Observational	109	33.0%	11.9%	55.1%	<0.001	0.018
Exp. & observational	3	33.3%	33.3%	33.3%	1.000	-

Heger, T. and Jeschke, J. M. 2014. The enemy release hypothesis as a hierarchy of hypotheses. – *Oikos* 123: 741–750.

Supplementary material Appendix 3

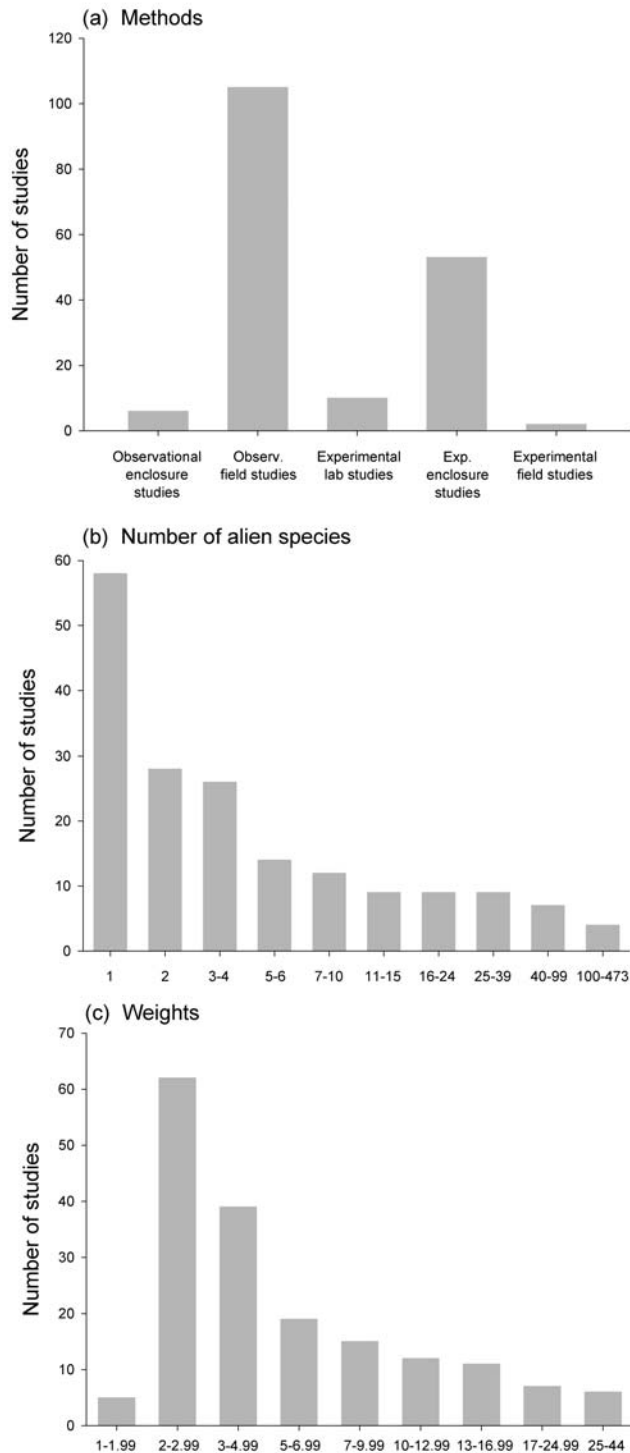


Figure A1. Numbers of empirical studies of the enemy release hypothesis identified in a systematic review, broken down according to (a) research method, (b) number of alien species studied, and (c) weights according to eq. 1.

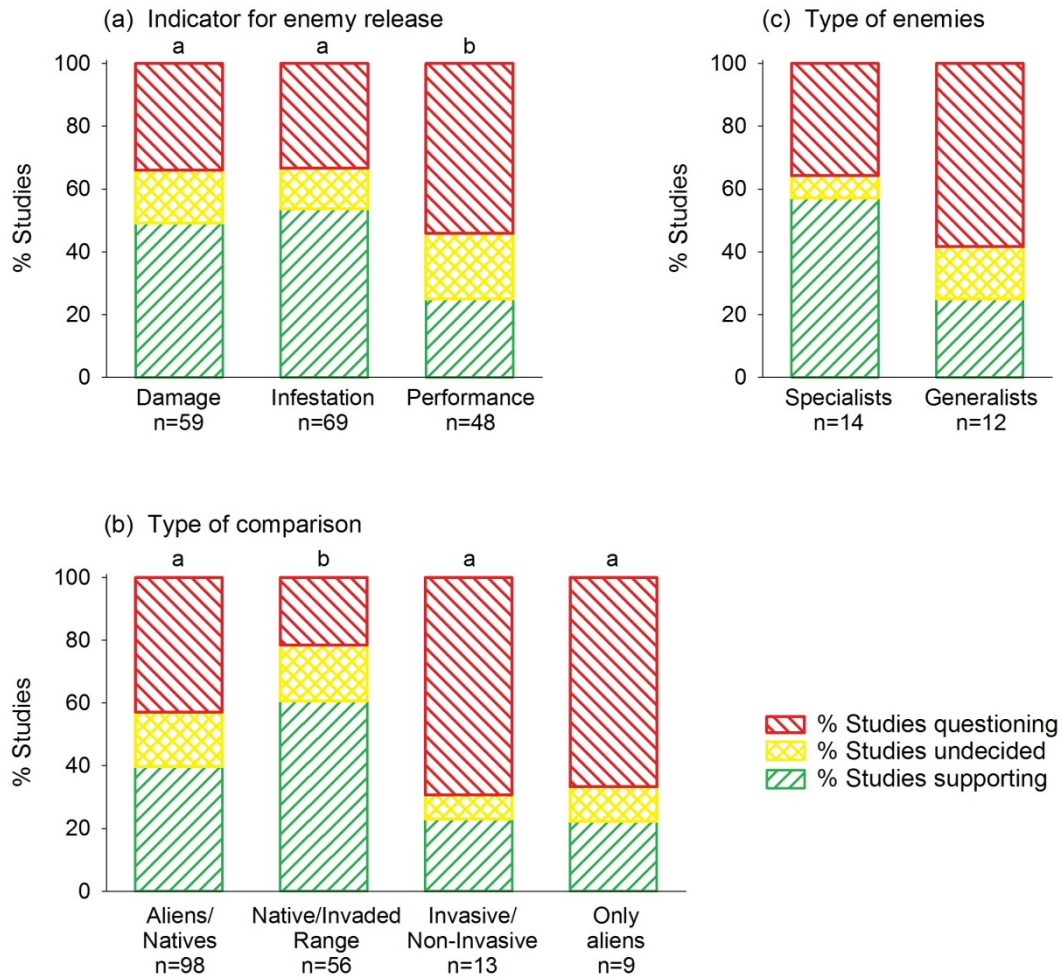


Figure A2. Level of empirical support for different sub-hypotheses of the enemy release hypothesis, differentiated according to (a) indicator for enemy release, (b) type of comparison, and (c) type of enemies – based on unweighted data. Letters on top of the bars indicate significant differences in empirical support (U tests, $p < 0.05$).

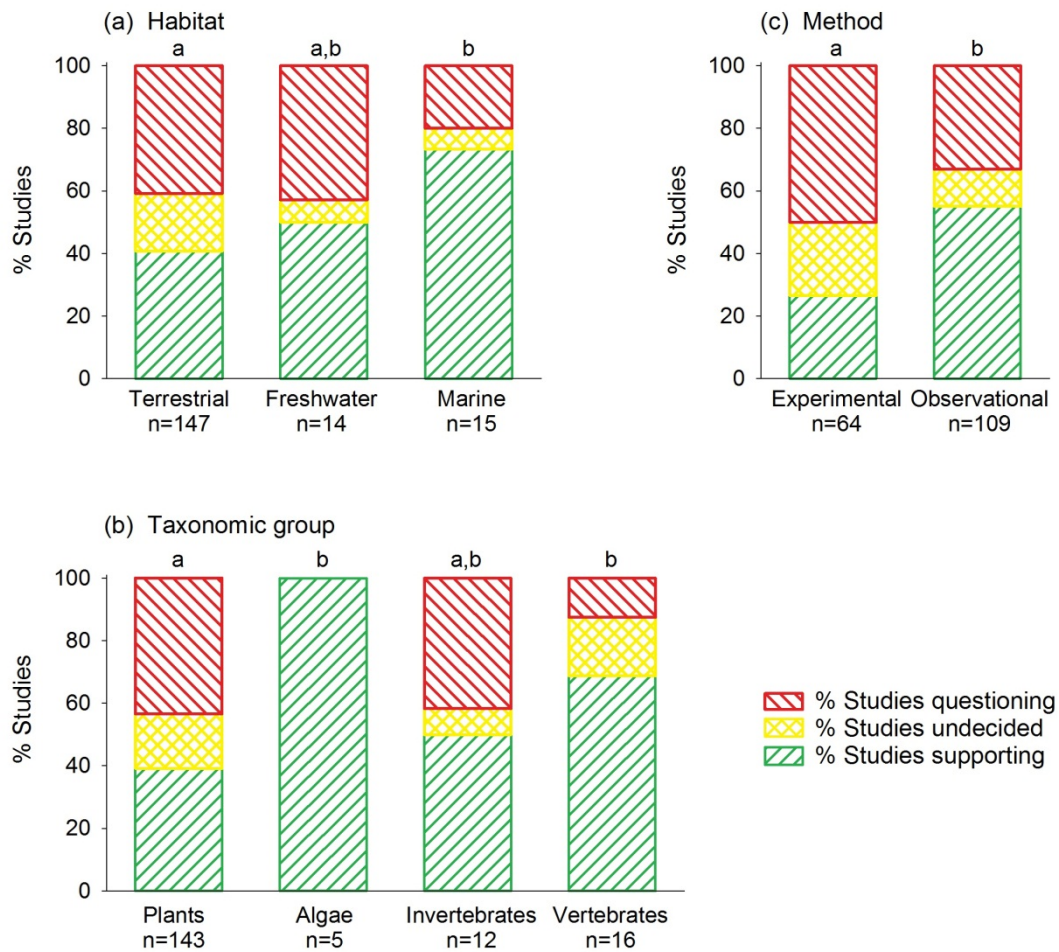


Figure A3. Level of empirical support for the enemy release hypothesis, differentiated according to (a) habitat type, (b) taxonomic group, and (c) research method – based on unweighted data. Letters on top of the bars indicate significant differences in empirical support (U tests, $p < 0.05$).

Supplementary material Appendix 4

Table A3. Weights and percentages of weighted evidence supporting (S), being undecided about (U), or questioning (Q) each sub-hypothesis of the enemy release hypothesis.

	Damage			Infestation			Performance			Total			
	S	U	Q	S	U	Q	S	U	Q	S	U	Q	
Aliens vs. natives	Generalists	0.00	13.86	0.00	0.00	30.30	0.00	67.86	0.00	0.00	112.01	0.00	0.00
		0.00%	0.00%	100.00%	0.00%	0.00%	100.00%	50.71%	28.88%	20.42%	30.72%	17.49%	51.79%
	Specialists	8.90	8.90	0.00	4.90	41.20	36.30	0.00	0.00	0.00	50.09	0.00	36.30
		100.00%	0.00%	0.00%	11.89%	0.00%	88.11%	0.00%	0.00%	0.00%	27.54%	0.00%	72.46%
	No differentiation	118.81	302.59	92.33	69.53	188.76	57.37	6.29	179.24	140.98	194.63	185.28	290.68
39.26%		30.51%	36.84%	32.77%	30.39%	3.51%	17.83%	78.66%	29.02%	27.63%	43.35%	670.59	
Total	127.71	325.34	106.18	74.43	260.26	123.96	40.70	247.10	154.84	242.84	204.88	384.98	
	39.25%	28.11%	32.64%	28.60%	23.77%	47.63%	16.47%	20.87%	62.66%	29.16%	24.60%	46.23%	
Aliens in native vs. invaded range	Generalists	0.00	0.00	0.00	0.00	4.00	4.00	0.00	0.00	0.00	4.00	0.00	4.00
		0.00%	0.00%	0.00%	0.00%	0.00%	100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	100.00%
	Specialists	0.00	0.00	0.00	10.00	12.00	0.00	0.00	0.00	0.00	10.00	2.00	0.00
		0.00%	0.00%	0.00%	83.33%	16.67%	0.00%	0.00%	0.00%	0.00%	83.33%	16.67%	0.00%
	No differentiation	20.00	30.00	4.00	97.49	113.49	10.00	24.83	44.83	16.00	142.32	28.00	18.00
66.67%		20.00%	13.33%	85.90%	5.29%	8.81%	55.39%	35.69%	8.92%	75.57%	14.87%	9.56%	
Total	20.00	30.00	4.00	107.49	129.49	14.00	24.83	44.83	4.00	152.32	30.00	22.00	
	66.67%	20.00%	13.33%	83.01%	6.18%	10.81%	55.39%	35.69%	8.92%	74.55%	14.68%	10.77%	
Invasive vs. non-invasive aliens	Generalists	5.29	5.29	0.00	0.00	0.00	0.00	9.80	0.00	9.80	5.29	0.00	9.80
		100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	100.00%	0.00%	35.07%	0.00%	64.93%
	Specialists	0.00	4.90	4.90	0.00	4.90	4.90	0.00	0.00	0.00	0.00	0.00	9.80
		0.00%	0.00%	100.00%	0.00%	0.00%	100.00%	0.00%	0.00%	0.00%	0.00%	0.00%	100.00%
	No differentiation	19.07	61.11	31.46	0.00	21.87	21.87	0.00	4.00	4.00	19.07	10.58	57.33
31.20%		17.32%	51.48%	0.00%	0.00%	100.00%	0.00%	0.00%	100.00%	21.92%	12.17%	65.91%	
Total	24.36	71.30	36.36	0.00	26.77	26.77	0.00	13.80	6.00	24.36	10.58	76.93	
	34.16%	14.84%	50.99%	0.00%	0.00%	100.00%	0.00%	0.00%	100.00%	21.78%	9.46%	68.76%	
Aliens with vs. without enemies	Generalists	n/a	n/a	n/a	n/a	n/a	n/a	6.93	0.00	0.00	6.93	0.00	0.00
		n/a	n/a	n/a	n/a	n/a	n/a	1.00	0.00	0.00	1.00	0.00	0.00
	Specialists	n/a	n/a	n/a	n/a	n/a	n/a	0.00	0.00	0.00	0.00	0.00	0.00
		n/a	n/a	n/a	n/a	n/a	n/a	0.00	0.00	0.00	0.00	0.00	0.00
	No differentiation	n/a	n/a	n/a	n/a	n/a	n/a	2.00	35.86	29.86	2.00	4.00	29.86
n/a		n/a	n/a	n/a	n/a	n/a	0.06	0.11	0.83	0.06	0.11	0.83	
Total	n/a	n/a	n/a	n/a	n/a	n/a	8.93	42.78	29.86	8.93	4.00	29.86	
	n/a	n/a	n/a	n/a	n/a	n/a	20.87%	9.35%	69.78%	20.87%	9.35%	69.78%	
Total	Generalists	5.29	19.15	13.86	0.00	34.30	34.30	41.34	84.59	23.65	46.63	19.60	71.81
		27.63%	0.00%	72.37%	0.00%	0.00%	100.00%	48.87%	23.17%	27.96%	33.78%	14.20%	52.02%
	Specialists	8.90	13.80	4.90	14.90	58.09	41.20	0.00	0.00	0.00	23.80	2.00	46.09
		64.49%	0.00%	35.51%	25.65%	3.44%	70.91%	0.00%	0.00%	0.00%	33.10%	2.78%	64.12%
	No differentiation	157.88	393.70	127.79	167.03	324.13	89.24	33.12	263.92	178.84	358.02	227.86	395.86
40.10%		27.44%	32.46%	51.53%	20.94%	27.53%	12.55%	51.96	67.76%	36.47%	23.21%	40.32%	
Total	172.07	426.65	146.54	181.92	416.52	164.73	74.46	348.51	202.49	428.45	249.46	513.76	
	40.33%	25.32%	34.35%	43.68%	16.77%	39.55%	21.36%	20.53%	58.10%	35.95%	20.93%	43.11%	

Table A4. Numbers and percentages of empirical tests supporting (S), being undecided about (U), or questioning (Q) each sub-hypothesis of the enemy release hypothesis.

	Damage			Infestation			Performance			Total			
	S	U	Q	S	U	Q	S	U	Q	S	U	Q	
Aliens vs. natives	Generalists	0	1	0	2	0	1	4	1	1	7	4	
		0.0%	0.0%	100.0%	0.0%	0.0%	100.0%	25.0%	50.0%	25.0%	14.3%	28.6%	57.1%
	Specialists	2	2	0	4	0	3	0	0	0	6	3	
		100.0%	0.0%	0.0%	25.0%	0.0%	75.0%	0.0%	0.0%	0.0%	50.0%	0.0%	50.0%
Aliens in native vs. invaded range	No differentiation	15	34	12	31	8	2	20	15	35	85	35	
		44.1%	20.6%	35.3%	58.1%	16.1%	25.8%	10.0%	15.0%	75.0%	41.2%	17.6%	41.2%
	Total	17	37	13	37	5	13	3	24	16	98	42	
		45.9%	18.9%	35.1%	51.4%	13.5%	35.1%	12.5%	20.8%	66.7%	39.8%	17.3%	42.9%
Invasive vs. non-invasive aliens	Generalists	0	0	0	2	0	0	0	0	0	2	2	
		0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	100.0%	
	Specialists	0	0	0	6	1	0	0	0	0	6	0	
		0.0%	0.0%	0.0%	83.3%	16.7%	0.0%	0.0%	0.0%	0.0%	83.3%	16.7%	0.0%
Aliens with vs. without enemies	No differentiation	9	14	3	21	5	7	13	2	29	48	10	
		64.3%	14.3%	21.4%	61.9%	14.3%	23.8%	53.8%	30.8%	15.4%	60.4%	18.8%	20.8%
	Total	9	14	3	29	4	7	7	13	2	56	12	
		64.3%	14.3%	21.4%	62.1%	13.8%	24.1%	53.8%	30.8%	15.4%	60.7%	17.9%	21.4%
Total	Generalists	1	1	0	0	0	0	1	0	1	2	1	
		100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	100.0%	100.0%	0.0%	100.0%	
	Specialists	0	0	1	1	0	1	0	0	0	2	2	
		0.0%	0.0%	100.0%	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	100.0%	
Total	No differentiation	2	6	3	2	2	0	1	1	2	9	6	
		33.3%	16.7%	50.0%	0.0%	0.0%	100.0%	0.0%	0.0%	100.0%	22.2%	66.7%	
	Total	3	8	4	3	0	3	0	2	2	13	9	
		37.5%	12.5%	50.0%	0.0%	0.0%	100.0%	0.0%	0.0%	100.0%	23.1%	7.7%	69.2%
Total	Generalists	n/a	n/a	n/a	n/a	n/a	1	1	0	1	1	0	
		n/a	n/a	n/a	n/a	n/a	100.0%	0.0%	0.0%	100.0%	0.0%	0.0%	
	Specialists	n/a	n/a	n/a	n/a	n/a	0	0	0	0	0	0	
		n/a	n/a	n/a	n/a	n/a	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	
Total	No differentiation	n/a	n/a	n/a	n/a	n/a	1	8	6	1	8	6	
		n/a	n/a	n/a	n/a	n/a	12.5%	12.5%	75.0%	12.5%	12.5%	75.0%	
	Total	n/a	n/a	n/a	n/a	n/a	2	9	6	2	9	6	
		n/a	n/a	n/a	n/a	n/a	22.2%	11.1%	66.7%	22.2%	11.1%	66.7%	
Total	Generalists	1	2	1	4	0	2	6	2	3	12	7	
		50.0%	0.0%	50.0%	0.0%	0.0%	100.0%	33.3%	33.3%	25.0%	16.7%	58.3%	
	Specialists	2	3	1	11	1	4	0	0	0	14	5	
		66.7%	0.0%	33.3%	54.5%	9.1%	36.4%	0.0%	0.0%	0.0%	57.1%	7.1%	35.7%
Total	No differentiation	26	54	18	54	15	10	42	24	67	150	57	
		48.1%	18.5%	33.3%	57.4%	14.8%	27.8%	23.8%	19.0%	57.1%	44.7%	17.3%	38.0%
	Total	29	59	20	69	9	23	12	48	26	176	69	
		49.2%	16.9%	33.9%	53.6%	13.0%	33.3%	25.0%	20.8%	54.2%	44.3%	16.5%	39.2%