Time to abandon the loss of dispersal ability hypothesis in island plants: A comment on García-Verdugo, Mairal, Monroy, Sajeva and Caujapé-Castells (2017)

Abstract

García-Verdugo et al. (2017) recently tested the loss of dispersal ability hypothesis in a wind-dispersed shrub from Southern Europe. Although the hypothesis has guided research for over 150 years, García-Verdugo et al. (2017) results failed to substantiate its central prediction—the loss of seed dispersal potential in island populations. Here, I highlight several additional limitations of the hypothesis. First, García-Verdugo et al. (2017) results are not unusual. Empirical support for the hypothesis is equivocal. Second, when reduced dispersal potential is documented, it may often evolve as a passive by-product of selection for large seeds, for reasons that are wholly unrelated to their dispersal. Third, the hypothesis does not readily apply to all plant dispersal modes, particularly plants that produce fleshy fruits. These issues advocate a fresh approach to the study of how selection shapes the evolution of dispersal potential on islands.

When asked to explain the existence of flightless animals on isolated islands, Darwin (1859) responded with a famous analogy involving shipwrecked sailors (Lomolino, 2010). He argued there were two strategies for sailors to survive a shipwreck. The first was to be a strong enough swimmer to reach the shore. The second was to be a poor swimmer and cling to the wreck. This second strategy has played in the minds of island biogeographers ever since and ultimately led to a long-standing hypothesis of how dispersal evolves on oceanic islands. The loss of dispersal ability hypothesis predicts that islands are initially colonized by individuals with relatively good powers of dispersal, but through time, island populations evolve poorer disperser ability to avoid being swept out to sea (see Cody & Overton, 1996).

In a recent issue of the Journal of Biogeography, García-Verdugo et al. (2017) provide an unusually thorough test of the loss of dispersal ability hypothesis in a wind-dispersed shrub, Periploca laevigata (Apocynaceae). They compared diaspore morphology and dispersal potential of P. laevigata populations in continental Europe and Africa to those on islands in both the Atlantic Ocean and Mediterranean Sea. They conducted molecular analyses to determine the age of island populations, as well as glasshouse experiments to establish whether diaspore morphology responds plastically to changes in environmental conditions.

García-Verdugo et al. (2017) results were inconsistent with the loss of dispersal ability hypothesis. Island populations of P. laevigata did not have reduced powers of dispersal relative to mainland populations. In fact, the opposite pattern was observed on the Cape Verde and western Canary Islands, which housed plants with comparatively high dispersal potential. The dispersal potential of island populations was also unrelated to when islands were colonized. Results from their common garden experiments showed that while fruit morphology varied plastically with environmental conditions, geographical patterns in dispersal potential were largely under genetic control. Therefore, evolution appears to have shaped the evolution of fruit form in P. laevigata, but not in the way predicted by the loss of dispersal hypothesis.

The loss of dispersal ability is usually considered to be a cornerstone of the ‘island syndrome’, a suite of attributes that delineate island biotas from those on continents (Grant, 1998; Lomolino, 2010; Whittaker & Fernández-Palacios, 2007). However, results from García-Verdugo et al. (2017) comprehensive study question its validity. What is more, their results are not unusual. Talavera, Arista, and Ortiz (2012) failed to find evidence for consistent losses of dispersal capacity in Rumex bucephalophorus (Polygonaceae) on some of the same islands studied by García-Verdugo et al. (2017). In a study of 27 plant species endemic to the Canary Islands, Vazačová and Münzbergová (2014) also failed to observe consistent support for the loss of dispersal capacity.

The purpose of this commentary is to discuss several additional shortcomings of the loss of dispersal ability hypothesis, aside from an emerging consensus that island plants are not necessarily poor dispersers. First, even when a loss of dispersal potential is observed, it does not necessarily support the loss of dispersal ability hypothesis. The loss of dispersal ability could arise as a passive by-product of selection for increased seed size, for reasons that are unrelated to seed dispersal distances.

This possibility is illustrated by another European study. Fresnillo and Ehlers (2008) tested the loss of dispersal ability hypothesis in three weed species inhabiting islands in the Danish Straits. Similar to García-Verdugo et al. (2017), they found that two species actually exhibited greater dispersal potential on islands, in stark contrast to predictions of the loss of dispersal ability hypothesis. However, the
third species investigated by Fresnillo and Ehlers (2008) was different. *Cirsium arvense* (Asteraceae) showed a reduction in dispersal potential on islands, as predicted by the loss of dispersal ability hypothesis. However, a closer look at the morphology of its diaspores suggests that a loss of dispersal ability could have evolved for reasons other than dispersal potential.

*Cirsium arvense* produces wind-dispersed diaspores that are comprised of a seed (achene) attached to a feathery plume (pappus), which carries seeds aloft on air currents. Differences in seed dispersal distances can therefore arise not only from changes in the size of plumes, but also from changes in the size of seeds, the payload plumes transport. Seed size is known to have a pronounced effect on a wide range of important demographic processes, including early seedling survivorship, tolerance to environmental hazards and competitive ability (Geritz, van der Meijden, & Metz, 1999; Harms & Dalling, 1997; Leishman & Westoby, 1994; Leishman, Wright, Moles, & Westoby, 2000; Lönnberg & Eriksson, 2013; Moles & Westoby, 2004; Rubio de Casas et al., 2017). This raises the possibility that differences in dispersal potential could evolve passively via selection for larger seeds, which can be advantageous for a variety of reasons at later life history stages.

Sherwin Carlquist (1966a,b), an early pioneer in the study of seed dispersal dynamics on islands, clearly recognized this mechanistic pathway towards reduced dispersal ability: “Extreme cases of loss of dispersability… feature increase in fruit size without concomitant increase in appendages which serve in dissemination” (page 46, Carlquist, 1966a). Furthermore, he reasoned, “a poorly functioning dispersal apparatus may be retained because it does not have a strongly negative selective value” (page 47, Carlquist, 1966a).

Fresnillo and Ehlers (2008) found that the loss of dispersal ability in *C. arvense* was not determined by decreased plume size. In fact, plume sizes tended to be bigger in island populations. Instead, declines in dispersal potential resulted from increases in seed size. These results are echoed by García-Verdugo et al. (2017), who found that *P. laevigata* populations on islands in Macronesia tended to produce larger seeds than mainland populations. Recent comparative work on species inhabiting a handful of islands in the Southwest Pacific found consistent support for seed gigantism, regardless of dispersal mode or life-form, suggesting that selection may consistently favour increased seed size in island plants (Kavanagh & Burns, 2014). However, it has yet to be established whether increased seed sizes are linked evolutionarily to dispersal capacity or some other factor.

In a global analysis of island bryophytes, Patiño et al. (2013) highlight an additional confounding effect in the dispersal potential of island plants. They found that island bryophytes typically produce larger spores than their mainland counterparts. In bryophytes, spore size directly determines their dispersal potential. Larger spores are heavier, so they travel in air currents for shorter periods than smaller spores, thus leading to shorter dispersal distances. Reductions in dispersal potential in island bryophytes evolved via selection for bigger spores, potentially for a variety of reasons, which may, or may not, be directly related to their dispersal potential. In particular, Patiño et al. (2013) show that the dispersal capacity of spores is confounded by breeding system, as asexual reproduction in bryophytes tends to result in larger spores than sexual reproduction. Therefore, the loss of dispersal potential in island bryophytes may stem from selection for increased asexual reproduction on isolated islands (i.e. Baker’s Law, see Pannell et al., 2015), rather than reduced dispersal potential. In a study of thousands of plant species, Grossenbacher et al. (2017) found that self-compatibility tends to be more prevalent on islands. A similarly extensive study on anemochorous plants on island across the globe could help establish whether the loss of dispersal ability is determined by changes in dispersal aides (e.g. the size of plumes), or changes in seed size.

A second problem with the loss of dispersal ability hypothesis is that it does not readily apply to some dispersal modes. Seed dispersal via ingestion by animals (endozoochory) is an exceedingly common dispersal mode in plants, and fleshy fruits have evolved independently on numerous occasions (Herrera, 2002). In fact, it is the predominant dispersal mode in woody plants, forested environments and in species that produce large seeds (Jordano, 2000). Any universal theory of how insularity shapes the dispersal potential of plants would obviously need to include this mode of seed dispersal. In wind-dispersed plants species, dispersal potential is determined by the relative sizes of seeds and dispersal aides (e.g. plumes or wings). However, in plants that produce fleshy fruits, the relationship between seed dispersal distances and dispersal aides (the quantity or quality of fruit pulp) is more complex. Despite decades of research, consistent relationships between fruit pulp and dispersal distances have yet to be established (see Herrera, 2002). Rather than being determined by the investment made by parent plants into dispersal aides, once fleshy fruits are consumed, seed dispersal distances are determined largely by the behaviour of the animals that ate them.

The chemical composition of fleshy fruits can influence gut retention times and therefore dispersal distances (Murray et al., 1994). Because frugivorous birds can only swallow fruits that are smaller than their gape size, restrictions in the size of frugivore assemblages associated with increased seed size might also curtail seed dispersal distances (see Burns, 2013). However, most fruit-eating animals inhabiting oceanic islands (e.g. birds, bats and reptiles) spend their entire lives in terrestrial environments. Seeds in the fruits they consume are therefore deposited in terrestrial environments. Although seabirds occasionally eat fleshy fruits, and they can sometimes be important dispersers of coastal plants (Calvino-Cancela, 2011), their relative contribution to terrestrial frugivore communities is typically negligible. As a result, seeds in fleshy fruits are unlikely to be deposited in the ocean. This cost of dispersal (see Bonte et al., 2012) forms the backbone of the loss of dispersal ability hypothesis. Its predictions hinge on the assumption that individuals with greater powers of dispersal are more likely to swept out to sea. On the other hand, individuals with poorer powers of dispersal are less likely to be dispersed at sea and are therefore at a selective advantage. Endozoochorous species appear to violate this assumption, and if so, the loss of dispersal ability hypothesis does not apply to them.

By providing testable predictions for how dispersal evolves on isolated islands, the loss of dispersal ability hypothesis has paved the
way towards a better understanding of general trends in island evolution. However, García-Verdugo et al. (2017) insightful study may be a turning point in our understanding of the dispersal capacity of island organisms. It now appears that the predictions of the loss of dispersal ability hypothesis are rarely upheld— island plants do not regularly evolve reduced dispersal potential. Furthermore, when the loss of dispersal ability is observed, it could have evolved passively, for reasons that are unrelated to dispersal potential. Lastly, its conceptual domain does not clearly encompass all modes of seed dispersal.

It is unclear whether the loss of dispersal ability hypothesis remains a valid hypothesis for island animals. Many flightless birds that are endemic to isolated islands evolved from volant ancestors (e.g. the dodo, Raphus cucullatus; kiwi, Apteryx spp.; moa-nalo, Thambo-chenini). Selection could have acted directly on their capacity to fly to lower the probability they would be lost at sea, in accordance with the loss of dispersal ability hypothesis. Indeed, many island birds develop a behavioural reluctance to cross water bodies prior to the evolution of morphological changes to their wings (Diamond, 1981; c.f. Imbert and Ronce (2001)). Alternatively, selection could have favoured large body size without concomitant increases in wing size (see Mitchell et al., 2014; Yonezawa et al., 2017).

Critically evaluating the loss of dispersal ability hypothesis need not be a dead end to future research on the topic. Instead, widening the scope of research beyond its predictions may help to accelerate interest, and progress, in our understanding of the evolution of dispersal potential in island populations. Many interesting questions remain unanswered. For example, is seed gigantism a repeated pattern in island evolution? If so, why might large seeds be selectively advantageous? How often does the evolution of seed gigantism lead to an indirect loss of dispersal ability? Answers to these and other important questions await a fresh approach to the problem.

ACKNOWLEDGEMENTS

I would like to thank Sonya Clegg, Ruben Heleno and an anonymous referee for insightful comments on an earlier draft of the manuscript.

ORCID

K.C. Burns http://orcid.org/0000-0002-4938-2877

K.C. Burns

School of Biological Sciences, Victoria University of Wellington,
Wellington, New Zealand

Correspondence

School of Biological Sciences, Victoria University of Wellington,
Wellington, New Zealand.

Email: kevin.burns@vuw.ac.nz

REFERENCES

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M.,…Travis, J. M. J. (2012). Costs of dispersal. Biological Reviews, 87, 290–312. https://doi.org/10.1111/j.1469-185X.2011.00201.x

Burns, K. C. (2013). What causes size coupling in fruit-frugivore interaction webs? Ecology, 94, 295–300. https://doi.org/10.1890/12-11611

Calvino-Cancela, M. (2011). Gulls (Laridae) as frugivores and seed dispersers. Plant Ecology, 212, 1149–1157. https://doi.org/10.1007/s11258-011-9894-2

Carlquist, S. (1966a). The biota of long-distance dispersal. II. Loss of dispersibility in Pacific Compositae. Evolution, 20, 30–48. https://doi.org/10.2307/1558646.https://www.jstor.org/stable/1558646.1

Carlquist, S. (1966b). The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. Brittonia, 18, 310–335. https://doi.org/10.2307/2805148

Cody, M. L., & Overton, J. McC. (1996). Short-term evolution of reduced dispersal in island plant populations. Journal of Ecology, 84, 53–61. https://doi.org/10.2307/2261699

Darwin, C. R. (1859). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (1st ed.). London: John Murray.

Diamond, J. M. (1981). Flightlessness and fear of flying in island species. Nature, 293(5833), 507. https://doi.org/10.1038/293507a0

Fresnillo, B., & Ehlers, B. K. (2008). Variation in dispersability among mainland and island populations of three wind dispersed plant species. Plant Systematics and Evolution, 270, 243–255. https://doi.org/10.1007/s00660-007-0615-1

García-Verdugo, C., Mairal, M., Monroy, P., Sajeva, M., & Caujapé-Castells, J. (2017). The loss of dispersal on islands hypothesis revisited: Implementing phyleogeography to investigate evolution of dispersal traits in Periploca (Apocynaceae). Journal of Biogeography, 44, 2595–2606. https://doi.org/10.1111/jbi.13050

Geritz, S. A., van der Meijden, E., & Metz, J. A. (1999). Evolutionary dynamics of seed size and seedling competitive ability. Theoretical Population Biology, 55, 324–343. https://doi.org/10.1006/tpbi.1998.1409

Grant, P. (1998). Patterns on islands and microevolution. In P. Grant (Ed.), Evolution of Islands (pp. 1–17). Oxford: Oxford University Press.

Grossenbacher, D. L., Brandvain, Y., Auld, J. R., Burd, M., Cheptou, P.-O., Conner, J. K.,…Goldberg, E. E. (2017). Self-compatibility is over-represented on islands. New Phytologist, 215, 469–478.

Harms, K. E., & Dalling, J. W. (1997). Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. Journal of Tropical Ecology, 13, 617–621. https://doi.org/10.1017/S0266474000010750

Herrera, C. M. (2002). Seed dispersal by vertebrates. In C. M. Herrera & O. Pellmyr (Eds.), Plant-animal interactions: An evolutionary approach (pp. 185–208). Oxford, UK: Blackwell Science.

Imbert, E., & Ronce, O. (2001). Phenotypic plasticity for dispersal ability in the seed heteromorphi Crepis sancta (Asteraceae). Oikos, 93, 126–134. https://doi.org/10.1034/j.1600-0706.2001.930114.x

Jordan, P. (2000). Fruits and frugivory. In R. S. Gallagher (Ed.), Seeds. The ecology of regeneration in plant communities (3rd ed., pp. 18–61). Oxfordshire, UK: CABI.

Kavanagh, P. H., & Burns, K. C. (2014). The repeated evolution of large seeds on islands. Proceedings of the Royal Society of London B: Biological Sciences, 281, 20140675. https://doi.org/10.1098 rspb.2014.0675

Leishman, M. R., & Westoby, M. (1994). The role of large seed size in shaded conditions: Experimental evidence. Functional Ecology, 8, 205–214. https://doi.org/10.2307/2389903

Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In M. Fenner (Ed.), Seeds: The
ecology of regeneration in plant communities (pp. 31–57). Oxfordshire, UK: CABI Publishing. https://doi.org/10.1079/9780851994321.0000
Lomolino, M. V. (2010). Four Darwinian themes on the origin, evolution and preservation of island life. Journal of Biogeography, 37, 985–994.
Lonnberg, K., & Eriksson, O. (2013). Rules of the seed size game: Contests between large-seeded and small-seeded species. Oikos, 122, 1080–1084. https://doi.org/10.1111/j.1600-0706.2012.0249.x
Mitchell, K. J., Llamas, B., Soubrier, J., Rawlence, N. J., Worthy, T. H., Wood, J., … Cooper, A. (2014). Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution. Science, 344, 898–900. https://doi.org/10.1126/science.1251981
Moles, A. T., & Westoby, M. (2004). What do seedlings die from and what are the implications for evolution of seed size? Oikos, 106, 193–199. https://doi.org/10.1111/j.0030-1299.2004.13101.x
Murray, K. G., Russell, S., Picone, C. M., Winnett-Murray, K., Sherwood, W., & Kuhlmann, M. L. (1994). Fruit laxatives and seed passage rates in frugivores: Consequences for plant reproductive success. Ecology, 75, 989–994. https://doi.org/10.2307/1939422
Pannell, J. R., Auld, J. R., Brandvain, Y., Burd, M., Busch, J. M., Cheptou, P.-O., … Winn, A. A. (2015). The scope of Baker’s law. New Phytologist, 208, 656–667. https://doi.org/10.1111/nph.13539
Patino, J., Bisang, I., Hedenäs, L., Dickse, C., Bjarnason, A. H., Ah-Peng, C., & Vanderpoorten, A. (2013). Baker’s law and the island syndromes in bryophytes. Journal of Ecology, 101, 1245–1255.
Rubio de Casas, R., Willis, C. G., Pearse, W. D., Baskin, C. C., Baskin, J. M., & Cavender-Bares, J. (2017). Global biogeography of seed dormancy is determined by seasonality and seed size: A case study in the legumes. New Phytologist, 214, 1527–1536. https://doi.org/10.1111/nph.14498
Talavera, M., Arista, M., & Ortiz, P. L. (2012). Evolution of dispersal traits in a biogeographical context: A study using the heterocarpic Rumex bucephalophorus as a model. Journal of Ecology, 100, 1194–1203. https://doi.org/10.1111/j.1365-2745.2012.01999.x
Vazacová, K., & Münzbergová, Z. (2014). Dispersal ability of island endemic plants: What can we learn using multiple dispersal traits? Flora, 209, 530–539.
Whittaker, R. J., & Fernández-Palacios, J. M. (2007). Island biogeography: Ecology, evolution, and conservation. Oxford: Oxford University Press.
Yonezawa, T., Segawa, T., Mori, H., Campos, P. F., Hongoh, Y., Endo, H., … Jin, H. (2017). Phylogenomics and morphology of extinct paleognaths reveal the origin and evolution of the ratites. Current Biology, 27, 68–77. https://doi.org/10.1016/j.cub.2016.10.029

How to cite this article: Burns KC. Time to abandon the loss of dispersal ability hypothesis in island plants: A comment on García-Verdugo, Mairal, Monroy, Sajeva and Caujapé-Castells (2017). J Biogeogr. 2018;45:1219–1222. https://doi.org/10.1111/jbi.13223