



# Insects With Survival Kits for Desiccation Tolerance Under Extreme Water Deficits

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The year 2002 marked the tercentenary of Antonie van Leeuwenhoek's discovery of desiccation tolerance in animals. This remarkable phenomenon to sustain 'life' in the absence of water can be revived upon return of hydrating conditions. Today, coping with climate change-related factors, especially temperature-humidity imbalance, is a global challenge. Under such adverse circumstances, desiccation tolerance remains a prime mechanism of several plants and a few animals to escape the hostile consequences of fluctuating hydroperiodicity patterns in their habitats. Among small animals, insects have demonstrated impressive resilience to dehydration and thrive under physiological water deficits without compromising on revival and survival upon rehydration. The focus of this review is to compile research insights on insect desiccation tolerance, gathered over the past several decades from numerous laboratories worldwide working on different insect groups. We provide a comparative overview of species-specific behavioral changes, adjustments in physiological biochemistry and cellular and molecular mechanisms as few of the noteworthy desiccation-responsive survival kits in insects. Finally, we highlight the role of insects as potential mechanistic models in tracking global warming which will form the basis for translational research to mitigate periods of climatic uncertainty predicted for the future.

**Keywords:** insect ecology, humidity, temperature, climate change, stress, desiccation tolerance, anhydrobiosis, adaptation

## INTRODUCTION

Long-term drought conditions leading to physiological water deficits are a threat to the survival and distribution of all organisms. To this notion, what comes as a delightful surprise is the demonstration of water loss mediated resurrection of apparently 'dead' organisms (Keilin, 1959). Such organisms have a remarkable ability of desiccation tolerance whereby they sustain cellular integrity in the desiccated form by activating unique physiological mechanisms (Clegg, 2001). Interestingly, this phase is reversible upon rehydration causing the revival and resumption of active metabolism. At present, global concerns include the challenges associated in coping with climatic stressors, especially the fallout due to humidity-temperature imbalance (Bellard et al., 2012; Boggs, 2016). Under the global sustainable development agendas<sup>1</sup>, research priorities on "life on land" (item#15) and "climate action" (item#13) have warranted attention. Among small animals, insects have proved to be reliable biological systems to anticipate cause-and-effect relations of climate change stressors (Addo-Bediako et al., 2001; Hoffmann and Todgham, 2010).

<sup>1</sup><https://www.un.org/sustainabledevelopment/sustainable-development-goals/>

This mini-review highlights the notable adaptive mechanisms employed by insects to evade dehydration bouts in their habitats. There have been a few reviews on similar topics (Watanabe, 2006; Cornette and Kikawada, 2011; Chown et al., 2011; Sogame and Kikawada, 2017); however, no recent competent review has emphasized on the profound diversity of hygropreference and associated strategies in insects. Most importantly, we discuss the desiccation tolerance profiles in insects irrespective of whether they possess a lower tolerance potential or are anhydrobiotic with a tolerance for severe water loss. These aspects have not been fully appreciated in the past, therefore, we aim to compile the diverse range of insect desiccation stress responses from a general perspective. Lastly, the present evaluation is by no means an exhaustive list of all desiccation tolerant insects; nonetheless, many case studies have been gathered within the ambit of insect water stress management.

## DRY BUT NOT DEAD

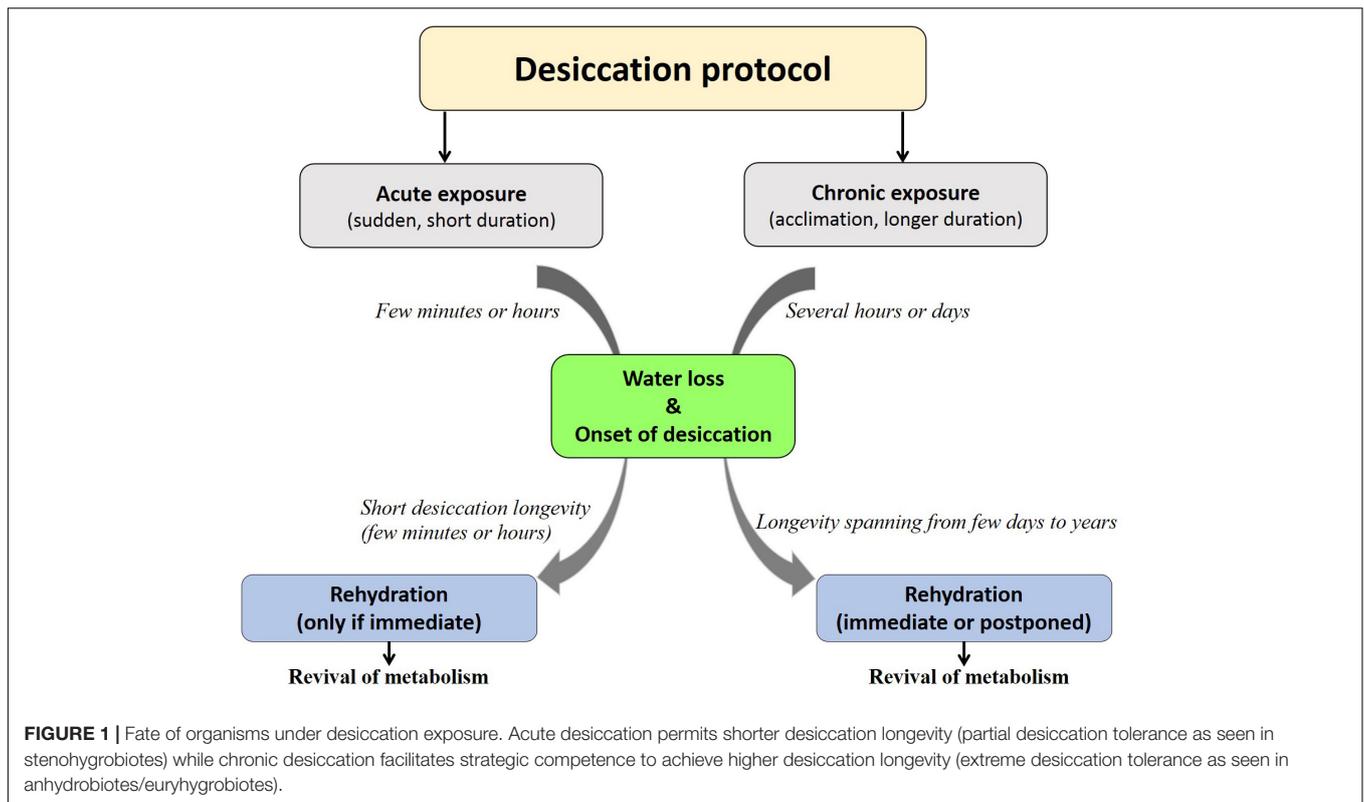
The documented history of desiccation tolerance dates back to 370 BC when Theophrastus described conditions necessary to store ‘dry seeds alive’ (Leprince and Buitink, 2015). Later, Antonie van Leeuwenhoek described his amazement over the dry dust containing ‘tiny dry animalcules’ that came to life within a few hours after being rehydrated with water (Keilin, 1959). Little did Leeuwenhoek know that his meticulous observations would form the basis of the latent phases of life. To describe this phenomenon, Giard (1894) coined the term ‘anhydrobiosis,’ an extreme form of desiccation tolerance which in Greek implies ‘life without water.’ ‘Desiccation avoidance’ and ‘desiccation tolerance’ are distinguishable phenomena (Pallarés et al., 2016). The former refers to the maintenance of water uptake and/or minimization of body water loss (e.g., *Folsomia candida*, Collembola: Isotomidae) while the latter includes organisms that can afford loss of water and sustain a dry form without compromising on revival upon rehydration (e.g., all anhydrobiotes). The threshold for tolerance of water loss is highly species-specific and striking differences in desiccation tolerance strategies and traits in congeneric insect species have been linked with their geographic locations and the frequency and duration of drought exposure (Marron et al., 2003; Strachan et al., 2015). However, this is not true in all insects such as few heliconiine butterflies (Lepidoptera: Nymphalidae) (Mazer and Appe, 2001). Contrary to the rationale that desert insects can withstand higher water loss than mesic species, the aquatic beetle, *Peltodytes muticus* (Coleoptera: Haliplidae) is known for its highest tolerance in comparison to the desert spider beetle, *Mezium affine* (Coleoptera: Ptinidae) (Pallarés et al., 2016). Closely related *Drosophila* species (Diptera: Drosophilidae) have evolved different water balance mechanisms as demonstrated in *D. nepalensis* vs. *D. takahashii* and *D. immigrans* vs. *D. nasuta* (Parkash et al., 2012a,b).

Each organism may have its specific threshold longevity in the dry state; however, desiccation tolerance by no means confers ‘immortality’ or infinite survival but is rather influenced by the

mode of desiccation, storage temperature, humidity and oxygen content (Tunnacliffe and Lapinski, 2003; Suemoto et al., 2004; Thorat and Nath, 2016). Depending on these factors, organisms display varying longevities in the desiccated form that may range from 1 day to several years (Figure 1). Notwithstanding these variations and by virtue of qualitative considerations, all such organisms have been considered as desiccation tolerant (Watanabe, 2006). To the best of our knowledge, a numerical method devised for grouping prokaryotes based on their degree of desiccation tolerance, was the first attempt made by Hernández et al. (2009). A recent study in animals proposed the ‘desiccation tolerance index’ (DTi) as a quantitative measure of endurance to desiccation stress (Thorat and Nath, 2016). This mathematical tool is based on the desiccation tolerance in nine oriental *Chironomus* species (Diptera: Chironomidae) which indicate varying degrees of the tolerance threshold based on their ecological habitats (Figure 2).

## ANHYDROBIOSIS: AN EXTREME CASE OF DESICCATION TOLERANCE

Anhydrobiosis is characterized by extreme body water loss, generally over 95% (Benoit, 2010; Sogame and Kikawada, 2017). Thus, anhydrobiosis refers to complete desiccation, unlike desiccation tolerance, which refers to partial dehydration. In this context, we would like to introduce the term, ‘euryhygrobiote’ for such organisms that show a wide range of dehydration tolerance with a high anhydrobiotic potential. Conversely, we coin the term ‘stenohygrobiote’ for organisms that have a narrow dehydration tolerance range and can bear water loss only up to a certain limit. The extremophilic midges (Diptera: Chironomidae), *Polypedilum vanderplanki* (Hinton, 1951) and *Belgica antarctica* (Lopez-Martinez et al., 2009) are valuable models in understanding the gamut of molecular and biochemical signatures that render them anhydrobiotic. Anhydrobiotes can also be referred to as ‘anhydrophiles’ in comparison to ‘anhydrophobes,’ which lack desiccation tolerance. *P. vanderplanki*, the largest known anhydrobiotic eukaryote, endures water content as low as 3% through a gradual and optimized desiccation regime to sustain the dry state for 17 years until rehydration (Cornette and Kikawada, 2011). A new related species, *Polypedilum pembai* sp.n. also possesses anhydrobiotic potential and shares a few overlapping mechanisms with *P. vanderplanki* (Cornette et al., 2017). Recent work from our laboratory has demonstrated that the tropical midge, *Chironomus ramosus* and the fruit fly, *Drosophila melanogaster* possess a lower ability to tolerate water loss in comparison to the anhydrobiotic midges (Thorat et al., 2017) and are therefore stenohygrobiotic. Among invertebrates, other well-studied non-insect anhydrobiotes include brine shrimps, tardigrades, rotifers and nematodes (Tunnacliffe and Lapinski, 2003; Rebecchi, 2013). Interestingly, desiccation tolerance also confers cross tolerance to a variety of other stressors through multiple physiological defenses including physical and cellular protection via antioxidants, compatible solutes, proteins and DNA repair (Gusev et al., 2010b).



## DESICCATION TOLERANCE STRATEGIES IN INSECTS

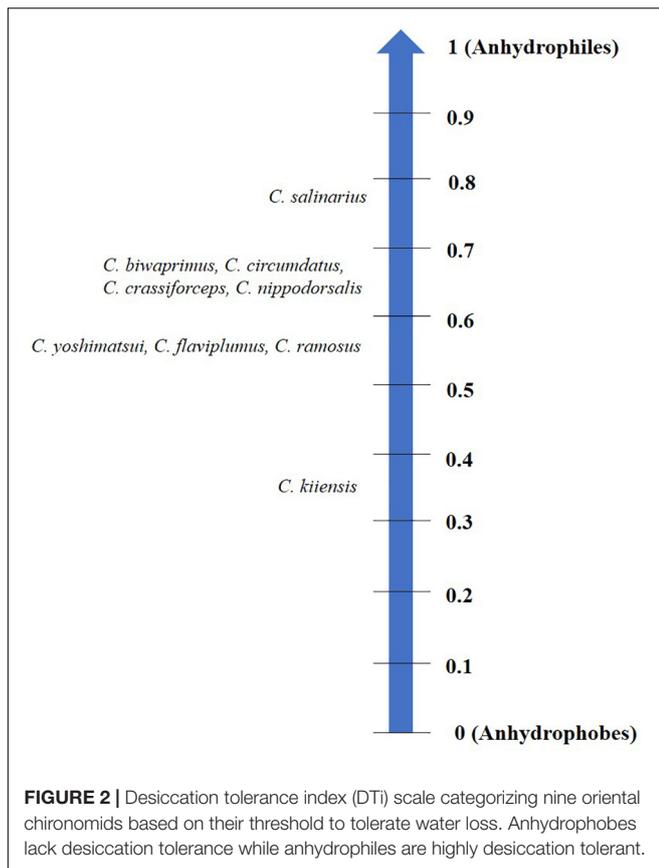
Environmental cues cause dormancy in insects, a phenomenon triggered by climatic signals including humidity, photoperiod, temperature, etc. (Diniz et al., 2017). Dormancy is further classified into diapause and quiescence. While diapause is a pre-programmed predictive strategy, quiescence is an immediate response to adverse environmental conditions (Denlinger, 1986; Danks, 2002). Aestivation, a form of consequential dormancy is the reason behind the aridity survival strategies of several insect species (Colvin, 1996; Benoit and Denlinger, 2007; North and Godfray, 2018). Anhydrobiosis (ametabolism) is an adaptation against physiological water stress, whereas dormancy is characterized by interrupted or reduced metabolic and hormonal activities (hypometabolism) in response to environmental cues (Watanabe, 2006).

While external milieu trigger desiccation stress responses, interoception is central to tolerance, survival and propagation of species. Below, we discuss a few of the striking and widely established strategies that constitute part of the desiccation tolerance approach of insects (Table 1).

### Behavior and Ecology

Hygrosensing abilities and behavioral responses suggest an evolutionary strategy for coping with water loss in insects (Chown et al., 2011). For instance, cockroaches show aggregation in order to control the water loss rate per

individual (Dambach and Goehlen, 1999). Similar observations in *Chironomus* larvae indicate a ‘clumping’ behavior, forming a single bunch to reduce evaporative body water loss (Thorat and Nath, unpublished). Some beetles exhibit bimodal activity patterns in order to escape the hottest hours of the day whereas others display fog-basking for moisture absorption from the surroundings (Bedick et al., 2006; Chown et al., 2011). Other striking evidences for aridity protection, come from niche construction behaviors such as the housing nests of chironomid midges, termite nests, domiciles of some thrips and insect galls (Kikawada et al., 2005; Gilberta, 2014; Zukowski and Su, 2017; Thorat and Nath, 2018). The cuticle is the first portal of water loss in insects and the differential desiccation tolerance patterns in *C. ramosus* vs. *D. melanogaster* and *P. vanderplanki* vs. *Paraborniola tonnoiri* (Diptera: Chironomidae) have been attributed to striking differences in their cuticular thickness (Nakahara et al., 2008; Thorat et al., 2017). Furthermore, in some insects, restructuring of the cuticle and morphological changes in spiracular features are crucial to minimize water loss. Such restructuring mechanisms are important because water is mainly lost passively and/or actively throughout spiracular respiration and cuticular transpiration (Hadley, 1994; Benoit and Denlinger, 2007; Benoit, 2010; Bazinet et al., 2010; Wadaka et al., 2016; Hidalgo et al., 2018; Ferveur et al., 2018). Other behavioral traits for desiccation protection such as the arrangement of egg laying (layering and density) in the nymphalid butterfly, *Chlosyne lacinia* (Lepidoptera: Nymphalidae), increases desiccation survival chances of eggs (Clark and Faeth, 1998).



## Development and Hormonal Regulation

Our current understanding on the desiccation-mediated developmental consequences in insects is rather fragmented. In the case of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae), desiccation does not exert significant effects on the average eclosion time (Xie and Zhang, 2007). In *C. ramosus* and *D. melanogaster*, modulations in 20-hydroxyecdysone affect recovery patterns and are linked with the desiccation-mediated delay in metamorphosis (Thorat and Nath, 2015; Thorat et al., 2016b). Interestingly, in *D. melanogaster*, despite the developmental heterochrony, the overall duration of postembryonic development of the life cycle remains almost unaltered. This is reminiscent of Waddington's 'canalization' as an adaptive buffer to adjust their life histories around optimal seasonal conditions (Thorat et al., 2016b). Life cycle and aging in desiccation tolerant animals has been categorized into three hypothetical models, the first, known as the 'Sleeping Beauty' model, implies that organisms totally disregard the entire time spent in the dry state, the second model considers that organisms register partial discount of the time spent in the dry state and the third model, whereby organisms record the exact time spent in the dry state, exhibiting non-extended longevity. *D. melanogaster* follows the Sleeping Beauty model similar to the non-insect anhydrobiotic tardigrade, *Milnesium tardigradum* (Schill, 2010; Thorat et al., 2016b). Variations in insect hormonal titres are key players

in synchronizing developmental changes in order to handle ecological ramifications of stressful environments such as hypoxia, high temperatures, starvation and sleep deprivation; however, investigations in the context of desiccation stress are warranted.

## Physiological Biochemistry

A longstanding biochemical adjustment of survival under dry conditions, is the ability of desiccation-responsive synthesis and accumulation of biomolecules including trehalose, mannitol, glycerol, Heat-Shock (HS) and Late Embryonic Abundant (LEA) proteins, proline, glycine-betaine, gamma aminobutyric acid, alanine, and glucosamine (Crowe and Madin, 1974; Tunnacliffe and Lapinski, 2003; Yoder et al., 2006; Kikawada et al., 2008; Philip et al., 2008; Benoit et al., 2009; Mitsumasa et al., 2010; Thorat et al., 2012; Hidalgo et al., 2014; Shukla et al., 2015, 2016, 2018; Yoshida et al., 2016; Thorat et al., 2017; Mazin et al., 2018). These compatible solutes not only offer protection to the drying tissues but also trigger various signaling responses during recovery. Although trehalose was considered indispensable for desiccation tolerance, recent compelling evidences have affirmed that trehalose accumulation may be completely absent in some organisms in which the desiccation protective role is taken up by other biomolecules (Tunnacliffe et al., 2005; Thorat et al., 2017). Differential physiological mechanisms involving carbohydrates, lipids and proteins are known to contribute to the invasive potential of three related *Ceratitidis* fly species (Diptera: Tephritidae) under episodic dehydration (Weldon et al., 2016). Osmoregulatory mechanisms in lepidopteran species have demonstrated the homeostatic control to readjust hemolymph osmolality triggered by body water loss (Willmer, 1980). Interestingly, eggs of *Acanthoscelides obtectus* (Coleoptera: Bruchidae) show water loss coping mechanisms that enhance egg tolerance and survival (Biemont et al., 1981). In the case of the flea beetle, *Longitarsus bethae* (Chrysomelidae: Alticinae), while low relative humidity has no influence on oviposition, aridity beyond a critical point is lethal for the eggs (Simelane, 2007). In contrast, egg desiccation did not affect embryo survival in xeric and mesic populations of the tobacco hawk moth, *Manduca sexta* (Lepidoptera: Sphingidae) (Potter and Woods, 2012).

## Antioxidant Defense

Ionic imbalance and changes in osmolality as a result of cellular water loss leads to the generation of reactive oxygen species (ROS) that are known to damage cellular macromolecules (Alpert, 2005; Benoit and Lopez-Martinez, 2012). Rebecchi (2013) has provided an excellent overview of the whole repertoire of antioxidant defenses under desiccation-responsive oxidative stress management in animals. *P. vanderplanki* shows the presence of both mitochondrial and cytosolic/extracellular superoxide dismutases (SODs) and abundant glutathione peroxidase and mitochondrial thioredoxin (Cornette et al., 2016; Nesmelov et al., 2016). Furthermore, genes that encode core components of enzymatic antioxidants in *P. nubifer* are similar to those in insects. However, in *P. vanderplanki* several groups of antioxidant genes have expanded (Gusev et al., 2014). In

**TABLE 1** | List of representative desiccation tolerant insects from different orders.

Order	Species	Life stage	Natural habitat	Reference
Collembola	<i>Folsomia candida</i>	Egg, larva, adult	Moist soil and sediments, leaf litter and decaying material	Sjursen et al., 2001; Holmstrup et al., 2002
	<i>Cryptopygus antarcticus</i> , <i>Friesea grisea</i>	Larva, adult	Moist Antarctic habitats	Alvarez et al., 1999; Hayward et al., 2004b; Elnitsky et al., 2008
	<i>Protaphorura tricampata</i> Adult		Meadows, mostly seashores	Holmstrup and Bayley, 2013
Ephemeroptera	<i>Cloeodes hydatation</i>	Larva	Pools, ephemeral, rain-filled rock pools and springs	Noite et al., 1996
Odonata	<i>Libellula depressa</i>	Larva	Still-water lakes and ponds (newly created ponds and well- vegetated ponds)	Rebora et al., 2007
Orthoptera	<i>Acheta domesticus</i>	Adult	Woodlands, caves, pastures, damp and soggy areas	McCluney and Date, 2008
	<i>Dianemobius nigrofasciatus</i>	Egg	Caves, fields, meadows, forests, grasslands, marshes and swamps.	Goto et al., 2008
	<i>Oedaleus senegalensis</i>	Egg, adult	Dry areas, annual grass communities, sandy soils	Colvin, 1996; Idrissa et al., 2008
Dictyoptera	<i>Periplaneta americana</i> , <i>Blattella germanica</i>	Nymph, adult	Humid spaces, cracks and crevices of porches, residential areas, temperate and tropical biomes, grasslands, rainforests and urban environments	Treherne and Willmer, 1975; Dambach and Goehlen, 1999
Phasmida	<i>Carausius morosus</i>	Egg, larva	Tropical forests, bushes and trees, garden plants, natural vegetation	Tichy, 1979
Plecoptera	<i>Protonemura intricata</i> ,	Egg, larva	Freshwater, terrestrial and shredders of decayed tree leaves	Harper and Hynes, 1970; Marten and Zwick, 1989; Lancaster et al., 2010
Isoptera	<i>Macrotermes carbonarius</i> , <i>M. gilvus</i>	Adult	Terrestrial, subterranean	Hu et al., 2012
	<i>Coptotermes formosanus</i> , <i>Neotermes jouteli</i> , <i>Cryptotermes cavifrons</i> , <i>C. brevis</i>	Adult	Terrestrial, subterranean, dampwood	Zukowski and Su, 2017
Dermaptera	<i>Labidura riparia</i>	Nymph, larva, adult	Terrestrial, dark and moist environments, cultured and uncultured farmlands, woodlands, margins of ponds and lakes	Kharboutli and Mack, 1993
Hemiptera	<i>Cryptotympana facialis</i> , <i>Graptosaltria nigrofuscata</i>	Nymph	Terrestrial, urban environments	Moriyama and Numata, 2010, 2011
	<i>Cimex lectularius</i>	Adult	Obligate blood feeders on humans	Benoit et al., 2007a
Trichoptera	<i>Lectrides varians</i>	Larva, pupa	Benthic, temperate lakes, streams, and ponds. Adults are terrestrial	Wickson et al., 2012
Lepidoptera	<i>Chlosyne lacinia</i>	Egg, Larva	Desert hills and woodlands	Clark and Faeth, 1998
	<i>Pieris brassicae</i> , <i>Aglais io</i> , <i>Heliconius charithonia</i>	Larva, Adult	Farms, tree trunks, walls and fences, in the vicinity of cruciferous plants	Willmer, 1980; Mazer and Appe, 2001
	<i>Manduca sexta</i>	Egg, larva	Facultative specialists on tobacco host plants	Rowley and Hanson, 2007; Davies et al., 2013
Hymenoptera	<i>Ceratosolen gallii</i> , <i>Ceratosolen arabicus</i>	Adult	Terrestrial on host fig trees	Warren et al., 2010
	<i>Apis mellifera</i>	Adult	Temperate, tropical deserts, dunes, savannas, grasslands, swamps, urban and agricultural areas.	Atmowidjojo et al., 1997
Diptera	<i>Aedes albopictus</i> , <i>Culex pipiens</i> , <i>Anopheles gambiae</i>	Egg, Larva, Adult	Egg, larva and pupa are aquatic (freshwater), adults are terrestrial	Sota and Mogi, 1992; Alto and Juliano, 2001; Hidalgo et al., 2014; Wadaka et al., 2016; Diniz et al., 2017
	<i>P. vanderplankii</i> , <i>P. pembai</i> , <i>B. antarctica</i> , <i>C. ramosus</i> , <i>C. kiensis</i> , <i>C. crassiforceps</i> , <i>C. nipodorsalis</i> , <i>C. biwaprimus</i> , <i>C. flaviplumus</i> , <i>C. salinarius</i> , <i>C. circumdatus</i> , <i>C. yoshimatsui</i>	Larva	Diverse aquatic habitats- African rock pools, rock pools of Malawi, Terrestrial Antarctic environments, tropical freshwater lakes and rivers, eutrophic lakes, rivers, ponds, artificial reservoirs and paddy fields	Suemoto et al., 2004; Benoit and Denlinger, 2007; Nakahara et al., 2008; Thorat and Nath, 2016; Thorat et al., 2017

(Continued)

TABLE 1 | Continued

Order	Species	Life stage	Natural habitat	Reference
	<i>Ceratitis capitata</i> , <i>C. cosyra</i> , <i>C. rosa</i> , <i>Bactrocera dorsalis</i>	Larva, adult	Fruit crop pest	Xie and Zhang, 2007; Weldon et al., 2016
	<i>Drosophila immigrans</i> , <i>D. pseudoobscura</i> , <i>D. hydei</i> , <i>D. mojavensis</i> , <i>D. birchii</i> , <i>D. nigrospiracula</i> , <i>D. nepalensis</i> , <i>D. takahashii</i> , <i>D. immigrans</i> , <i>D. nasuta</i> , <i>D. melanogaster</i> , <i>D. simulans</i>	Larva, adult	Deserts, tropical rainforest, cities, swamps, alpine zones, on decaying plant and fungal material	Hoffmann and Parsons, 1989; Davidson, 1990; Gibbs and Matzkin, 2001; Marron et al., 2003; Hoffmann et al., 2003; Bazinet et al., 2010; Thorat et al., 2012; Parkash et al., 2012a,b; Davies et al., 2013; Thorat et al., 2016b; Ferveur et al., 2018
	<i>Sarcophaga bullata</i>	Larva	Rural and urban environments, commonly found in houses and indoor dwellings	Yoder et al., 2006
Coleoptera	<i>Acanthoscelides obtectus</i>	Egg	Granivore, infesting seeds or beans and living inside them	Biemont et al., 1981
	<i>Longitarsus bethae</i>	Egg	Soil-dwelling, root-feeding on the host plant, <i>Lantana camara</i>	Simelane, 2007
	<i>Peltodytes muticus</i> , <i>Mezium affine</i> , <i>Enochrus halophilus</i> , <i>E. politus</i> , <i>E. bicolor</i> , <i>E. jesuarrubasi</i>	Adult	Aquatic, temporary-lentic or intermittent-lotic water bodies, deserts	Arlian and Staiger, 1979; Pallarés et al., 2016
Siphonaptera	<i>Spilopsyllus cuniculi</i>	Egg, larva, pupa, adult	External parasite of rabbits	Cooke and Skewes, 1988
	<i>Ctenocephalides felis</i>	Egg, larva, pupa, adult	External parasite of cats	Silverman and Rust, 1983

contrast, SOD serves as the major antioxidant in *B. antarctica* (Benoit and Lopez-Martinez, 2012). Recently, the role of unconventional antioxidant molecules such as trehalose, proline, polyamines and polyols has gained attention (Goyal et al., 2004; Schill et al., 2009; Benoit and Lopez-Martinez, 2012). Trehalose, in particular, has been confirmed for its ROS-scavenging ability in SOD-deficient yeast cells and plants (Kranner and Birtič, 2005; França et al., 2007). Using the advantage of molecular genetic tools in *Drosophila* and a simple, non-invasive method of whole larval real-time imaging, Thorat et al. (2016a) have demonstrated for the first time that during desiccation, trehalose in collaboration with SOD is involved in the maintenance of redox homeostasis in insects.

## Molecular and Evolutionary Biology

Cellular decline in water levels serves as a cue to elicit defensive-responses of molecular indicators. Among the molecular responses mediated *via* proteins, Hsps, namely, smHsp, Hsp70 and Hsp90 have been linked with desiccation survival in insects (Tammariello et al., 1999; Sjrursen et al., 2001; Hayward et al., 2004a; Benoit et al., 2009; Benoit, 2010). LEA proteins are another group of upregulated molecules that act as molecular shields to protect other proteins and bio-membranes against aggregation and denaturation resulting from drying (Goyal et al., 2005; Sogame and Kikawada, 2017). Interestingly, however, *B. antarctica* lacks genes encoding LEA proteins and Hsps are apparently not involved in conferring desiccation tolerance (Philip et al., 2008). Instead, metabolite synthesis and membrane phospholipids, distinct contractile and cytoskeletal protein patterns and aquaporins are among the key players essential for successful anhydrobiosis in the Antarctic midge

(Benoit et al., 2007b; Michaud et al., 2008; Li et al., 2009; Teets et al., 2012; Kelley et al., 2014). In addition, desiccation response was shown to upregulate 'Frost,' 'Desi' and 'smp-30' genes whereas 'Desat2' was downregulated during post-desiccation recovery (Sinclair et al., 2007; Kawano et al., 2010). Metabolic fingerprint comparisons in mosquitoes have highlighted specific metabolic alterations, enabling them to survive seasonal aridity (Hidalgo et al., 2015). Diapause in *Aedes albopictus* (Diptera: Culicidae) promotes desiccation survival by overexpression of a transcript involved in lipid storage with a concomitant increase in hydrocarbon levels (Diniz et al., 2017). Seminal contributions from Davies et al. (2014) have deepened our understanding on the neuroendocrine regulation of salt and water balance in insects (Luan et al., 2015). Recently, the importance of capa neuropeptides as anti-diuretic hormones have been identified in *D. melanogaster* and is postulated to be a part of desiccation tolerance mechanisms in other insects as well (Davies et al., 2013; Terhzaz et al., 2015).

## CONCLUSION

Adaptive mechanisms vary among organisms based on their ecological and evolutionary background. Thus, stress tolerance physiology is bound to vary even among closely related species and therefore cannot be generalized. In addition, variations in desiccation tolerance physiology is often a result of the desiccation protocols (acute/chronic) employed. It might therefore be possible to judge the desiccation tolerance or anhydrobiotic potential of organisms in the true sense, only when they are studied under a common denominator of reproducible protocols. Nature has a vast array of tactics

to safeguard its biodiversity and therefore, exploration of other aridity-induced mechanisms in known and unknown desiccation tolerant organisms will give way to our holistic understanding of the diversity in tolerance patterns from an evolutionary, ecological, physiological, cellular and molecular perspective. As reviewed here, although several molecular and biochemical underpinnings of desiccation tolerance in insects are thoroughly studied and well-established, an understanding of some other basic mechanisms remain elusive. For instance, there is a lack of information on the status of the immune responses elicited during desiccation survival. Another neglected area is the understanding of the neuronal basis governing recovery from desiccation that leads to the reactivation of coordinated sensory circuits. As an example, Pflüger and colleagues have determined the role of insect neurotransmitters in modulating multiple physiological and behavioral processes and have emphasized the involvement of biogenic amines under heat, mechanical stress, starvation and chemicals in insects (Verlinden et al., 2010). Similar studies on physiological water deficits in insects can hold great promise for translational research.

The role of insects as reliable mechanistic models presents endless research possibilities for the prediction of the consequences of climate change. The extreme desiccation tolerance of *P. vanderplanki* has been exploited as a prototype insect system for investigating the influence of spaceflight environments on life processes (Gusev et al., 2010a). Furthermore, the knowledge of insect desiccation biology offers ample ideas for exciting biomedical and pharmaceutical applications, e.g., anhydrobiotic engineering that targets at improving desiccation tolerance of desiccation-sensitive species, including humans (de Castro et al., 2000; Watanabe et al., 2016). These and many other applications that might have been previously viewed as science fiction, are now possible because of our knowledge of insect responses to water scarcity.

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Thus, research in desiccation stress response biology has come a long way from curiosity-driven explorations to present day technology-driven applications. Therefore, we hope that this review will trigger impetus for the development of methods and technology to mitigate the consequences of climate change in human and non-human biota.

## AUTHOR CONTRIBUTIONS

LT and BN designed the review layout. LT prepared the manuscript draft, table, and figures. BN revised the manuscript with critical inputs. BN and LT approved the final version of the manuscript.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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